DEC 2 0 '26

JOURNAL OF ANATOMY

ORIGINALLY THE JOURNAL OF ANATOMY AND PHYSIOLOGY

CONDUCTED ON BEHALF OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND BY

PROFESSOR E. BARCLAY-SMITH, UNIVERSITY OF LONDON
PROFESSOR J. P. HILL, UNIVERSITY OF LONDON
PROFESSOR ARTHUR ROBINSON, UNIVERSITY OF EDINBURGH
PROFESSOR WILLIAM WRIGHT, UNIVERSITY OF LONDON
PROFESSOR SIR ARTHUR KEITH, ROYAL COLLEGE OF SURGEONS

LINCOLN'S-INN-FIELDS, LONDON, W.C. 2.

VOLUME LXI
PART I
OCTOBER 1926

Entered at New York Post Office as Second Class Matter

(All Rights reserved)

CAMBRIDGE UNIVERSITY PRESS
LONDON: FETTER LANE, E.C. 4

ALSO

H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1
WHELDON AND WESLEY, LTD., 2-4, ARTHUR ST., NEW OXFORD ST., W.C. 2
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
(AGENTS FOR THE UNITED STATES)
BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

Price Ten Shillings net

PRINTED IN GREAT BRITAIN

BIOMETRIKA

A Journal for the Statistical Study of Biological Problems

Volume XVIII, Parts I & II. July, [illegible] (Inclusive of postage)

CONTENTS

"Biometrika" Portrait Series. No. III. [illegible]. A Third Study of the English Skull with Special Reference to the Mediæval Period and to Modern Examples. By [illegible]. (With six diagrams and six maps in the text, six plates and folding table.) [illegible]. A Third Study of the Craniology of England and Scotland [illegible] Periods. By [illegible]. (With six diagrams and six plates in pocket.) [illegible]. Anthropometric Observations on Skulls in London Museums. [illegible]. By [illegible], D.Sc. [illegible] and six plates in pocket.) [illegible]. [illegible] Anthropometric and Historic Times. By [illegible]. [illegible] Old Celtic Likeness. By Karl Pearson, F.R.S. [illegible] Remains Recently Found in St Magnus Cathedral, Kirkwall, Orkney. By Professor R. W. [illegible], D.Sc. (With [illegible] Figures in the text and four plates.) VI. The Corpuscle Problem. Second [illegible]. By S. D. Wicksell, Lund. VII. Further Note on the Distribution of [illegible] Form in a Normal Population. By Egon S. Pearson, D.Sc. (With seven diagrams in the text.) [illegible]. Head Measurements and Mental Agility. Women. By [illegible]. With two diagrams in the text and one folding table.) [illegible]. On the Power of [illegible] and Reaction Time to Sight and Sound. When [illegible]. By E. Hanson, M.D. [illegible]. By Karl Pearson. (With two diagrams in the text and one folding table.)

Miscellanea: (i) On Rayleigh's Generalised [illegible]. By [illegible], M.A. (ii) On the Linear Correlation Ratio in the Case of Certain [illegible]. By J. S. Mitchell, Ph.D., Johns Hopkins University. (iii) On the Average [illegible]. By Karl Pearson, F.R.S.

The subscription price, payable in advance, is 40s. net [illegible] (postage and postage); single numbers 16s. net. Owing to the scarcity of early volumes [illegible] now be charged for complete sets. Vols. I to XVII: Bound in buckram cases, in [illegible] cases may still be obtained at cheaper prices. Standard buckram cases with Darwin [illegible] postage per volume. Index to Vols. I to V, 2s. net. Index to Vols. I to XV, 5s. net. [illegible] payable to Professor Karl Pearson and sent to the Secretary, Biometric Laboratory, [illegible] don, W.C.1, to whom all orders for series and single copies should be addressed. [illegible] ly stamped and should be crossed "Biometrika Account."

Issued by

THE BIOMETRIC LA[illegible]

University College, [illegible]

The University of Chicago Press

A LABORATORY MANUAL FOR COMPARATIVE VERTEBRATE ANATOMY. By L. H. Hyman. [illegible]. With 69 text-figures. Large Royal 8vo. 12s 6d net

GENERAL CYTOLOGY. A Textbook of Cell Structure and Function for Students of Biology and Medicine. [illegible] E. V. Cowdry. Profusely illustrated. Royal 8vo. 37s 6d net

HISTORY AND BIBLIOGRAPHY OF [illegible]OMIC ILLUSTRATION. By Ludwig Choulant. Translated [illegible] with notes and biography, by Mortimer Frank. Many illustrations. [illegible]

THE ORIGIN AND DEVELOPMENT [illegible] OF THE NERVOUS SYSTEM FROM A PHYSIOLOGICAL VIEWPOINT. By Charles Manning Child. With [illegible] figures. 12mo. [illegible] net. [illegible] of Chicago Science Series

STUDIES IN THE PALEOPATHOLOGY OF EGYPT. By Sir Marc Armand Ruffer. With a frontispiece, [illegible] text-figure. Large Royal 8vo. 37s 6d net

Cambridge University P[illegible]don, E.C.4

JOURNAL OF ANATOMY

THE OCCIPITAL LOBE IN THE BRAIN OF THE CHINESE WITH SPECIAL REFERENCE TO THE SULCUS LUNATUS

By JOSEPH L. SHELLSHEAR
Hongkong

INTRODUCTION

The important part which the sense of vision has played in the evolution of man makes it a matter of peculiar interest to investigate and compare the occipital region in the brain of the different races of mankind. Not only has Elliot Smith (9) revealed to us the probable path which man has trod in his upward march, and the rôle which vision has played in this advance; but also he has given us, by his investigations into the brain of the primates, the first clear knowledge of the homologies that may be instituted between the sulcal pattern of the human brain and that of the anthropoid apes. By the identification of the "Affenspalte" in the human brain (1) and by clearly distinguishing the difference in nature between the anterior and posterior calcarine sulci (5) he has paved the way for a more definite understanding of the differences that exist in the races of mankind in this important region.

It has been my good fortune, since coming to Hongkong, to have examined a very large number of Chinese brains in the fresh condition, as well as in the preserved state; and the present research is founded on the examination of over 400 specimens. While it is unlikely that this heterogeneous group represents a pure race, the features of the occipital region differ, in certain particulars, from anything hitherto recorded, and suggest that the departures from the recorded types are explainable on the grounds that there is such a thing as a Mongoloid type of brain; and that in all probability this type is distinctive.

The most outstanding feature in the occipital region of the brain in the anthropoids is the "Affenspalte," or sulcus lunatus occipitalis. Its frequent, if not universal, presence in the human brain has been pointed out by Elliot Smith (1); and his claim that this sulcus in man is the definite homologue of the sulcus lunatus in the anthropoid apes has been almost universally accepted. The present work on the brain of the Chinese can leave no doubt as to the correctness of his findings. Hulshoff Pol (10) and (11), however, would dispute his interpretation on the ground that he has not produced confirmatory embryological evidence, and would suggest that the older description of Gratiolet, with modification, should be retained. The condition of affairs in the brain of the Chinese would indicate that Pol has not examined the brains

of other races than the European, and that he has not looked for his confirmatory embryological evidence in the embryos of such a race as the Egyptian or the Chinese. Disagreement will also be found with his statement that "Elliot Smith's description is so vague that each sulcus on the occipital lobe can be taken for the sulcus lunatus."

The precision of Elliot Smith's description(6), not only of the sulcus lunatus, but also of such sulci as the sulcus paramesialis and the sulcus praelunatus, has made the interpretation of the brain of the Chinese so easy.

The Sulcus Lunatus

In the course of its evolution, the occipital lobe alters in its general appearance so far as the form of the various sulci is concerned, but the identity of these sulci remains apparent, not only in the brain of the apes, but also in the majority of human brains. The part played by the sense of vision in the attainment of the higher intellectual powers is expressed in the extent of the expansion of those areas of the cerebral cortex which Elliot Smith has termed para- and peristriate(6). This expansion around the periphery of the striate cortex causes a rolling back of the occipital operculum, and the consequent exposure of the sulci found on the anterior wall of the fossa lunata. In some cases in the orang outan this rolling back exposes the dorsal part of the sulcus parieto-occipitalis, but the sulcus occipitalis transversus remains hidden from view.

In the most primitive types of human brain thus far described, the rolling back has been continued a step further, and has brought about the full exposure of the sulcus occipitalis transversus on the surface, separated from the opening of the fossa, or sulcus lunatus, by a transverse gyrus of variable width. Retzius(12) has depicted a human brain in which the outer limb of the sulcus occipitalis transversus reaches the sulcus lunatus, but has failed to recognise the identity of the sulcus lunatus, regarding it as a "Halbringform."

Fig. 1 depicts the form and relations of the right sulcus lunatus (Sulc. Lun.) in the orang outan. It is seen to be a curved sulcus extending from the mesial almost to the tentorial border; the posterior lip of the operculum limits the stria of Gennari: laterally it is associated with a short horizontal sulcus—the sulcus praelunatus (*S. Pl.*). Within the concavity of the sulcus lie the Y-shaped sulcus occipitalis superior (*S.O.S.*) and the sulcus occipitalis inferior (*S.O.I.*). The sulcus occipitalis transversus is completely hidden on the anterior wall of the fossa lunata.

Such are the characters by which the sulcus lunatus is to be recognised (Davidson Black(13)).

Fig. 2, taken from the right hemisphere of a Chinese child of three years, reveals a configuration of sulci that differs from that seen in the orang outan only in minor details. It illustrates the most primitive type of human brain so far described. The sulcus lunatus is of somewhat different shape, and is not so extensive as it is in the orang; but it is nevertheless a prominent

feature of the occipital region, whose identity must be regarded as established by the fact that the posterior lip forms a well-marked operculum and that this lip exactly limits the stria of Gennari. The point of junction of the sulcus paroccipitalis (*S. Paro.*) with the sulcus occipitalis transversus (*S.O.T.*) is in great part hidden from view. The submergence, however, is not complete, for the ends of the two limbs of the transverse occipital sulcus can be seen emerging from under cover of the operculum. Fig. 3 gives an idea of the appearance of the specimen with the operculum drawn back. Associated with the *inner portion* of the sulcus lunatus, the sulcus paramesialis is seen passing forwards and inwards to join the sulcus parieto-occipitalis: laterally the sulcus praelunatus (fig. 2, *S. Pl.*) passes forwards from the *outer portion* of the sulcus lunatus towards the inferior parietal lobule: and finally, within the concavity of the sulcus are found the sulci occipitalis superior et inferior (*S.O.S.* and *S.O.I.*).

Every criterion for identifying the sulcus lunatus is fulfilled; but in order to dispel any doubt which may be raised from the embryological evidence, fig. 4 is given to show the brain of a Chinese embryo, in which the sulcus lunatus is plainly seen.

The expressions "inner and outer portions of the lunate sulcus" have been used above. On drawing back the operculum, one sees, not only in the human brain, but also in the brain of the orang, that, in the depths of the folding which forms the operculum, the inner portion of the sulcus lunatus is separated from the outer portion. The inner segment lies on the posterior wall of the operculum and differs from the outer portion in that it bears a different relation to the stria of Gennari. It is a sulcus which posteriorly lies within the striate area and anteriorly lies in front of it (fig. 3). It is connected with the sulcus paramesialis. Very frequently the cortex that separates the two elements comes to the surface; and then there appears a triradiate sulcus on the mesial border consisting of the inner portion of the sulcus lunatus and the sulcus paramesialis. The strip of cortex is the "pli de passage supérieur of Gratiolet." The very feature which Pol would make use of to disprove Elliot Smith's work becomes a most useful guide for homologising the sulcus lunatus. I propose to name this inner portion the "pars medialis sulci lunati" (figs. 6, 10, 11, 24, 25 *b*, 26 and 27).

Fig. 5 gives the appearance of sagittal sections taken through the lines *a–b* in figs. 1 and 8. In these sections the pars mesialis sulcus lunatus is seen on the posterior wall of the fossa.

The meaning of the arrangement of the sulci in fig. 6, now becomes apparent. This brain was taken from a Chinese child, four years of age, who had a complete transposition of the viscera. The sulcus occipitalis transversus is completely hidden on the anterior wall of the lunate fossa. The pars medialis sulci lunati is a separate element joined to the sulcus paramesialis. The sulcus lunatus proper might readily be confused with the sulcus occipitalis transversus. It is shown as a crescent-shaped sulcus lying obliquely across the occipital region. There can be no doubt, however, about the identity. The

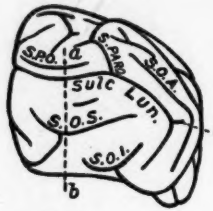


Fig. 1.

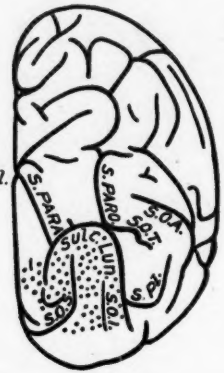


Fig. 2.

Fig. 3.

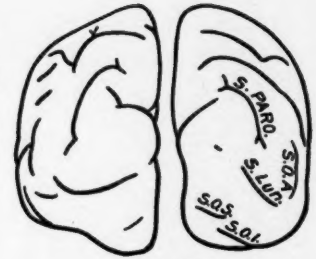


Fig. 4.

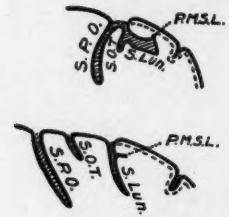


Fig. 5.

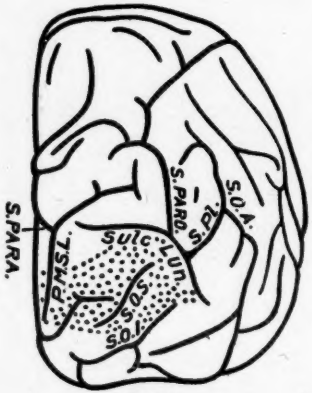


Fig. 6.

Fig. 7.

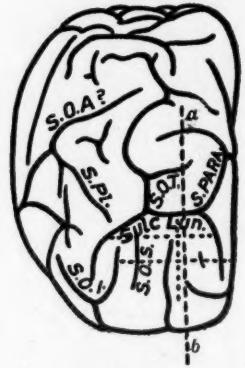


Fig. 8.

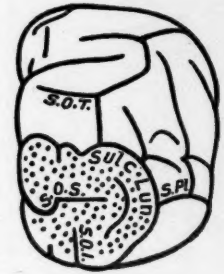


Fig. 9.

Fig. 6. Fig. 7. Fig. 8. Fig. 9.

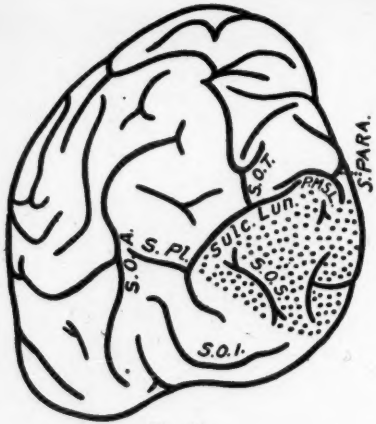


Fig. 10.

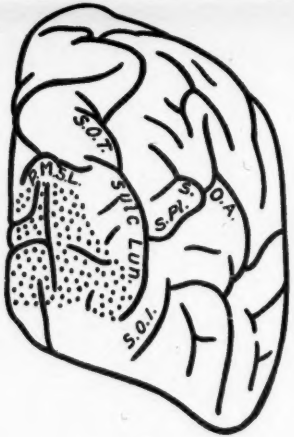


Fig. 11.

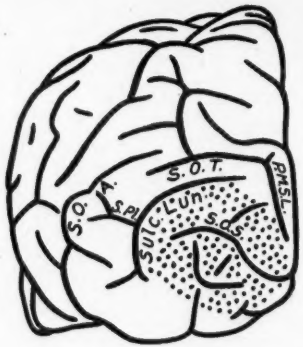


Fig. 12.

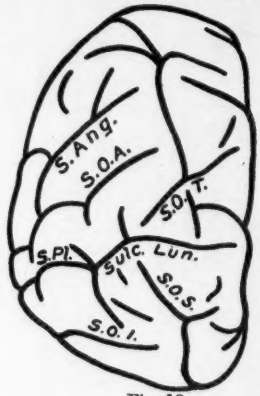


Fig. 13.

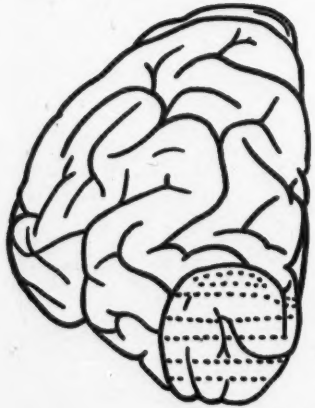


Fig. 14.

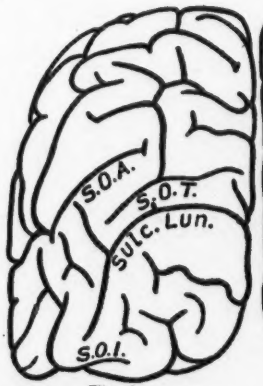


Fig. 15*a*.

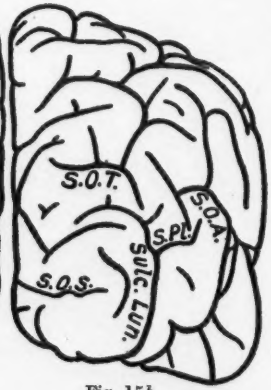


Fig. 15*b*.

striate cortex is definitely limited by the posterior lip of the sulcus (a relationship which is never found in the case of the transverse occipital sulcus). The posterior lip forms a well-marked operculum which covers a considerable area of cortex; the sulcus praelunatus is typically arranged, passing forwards to join the sulcus occipitalis anterior (*S.O.A.*, frequently described as the termination of the sulcus temporalis medius); finally on the anterior wall of the fossa, the sulcus occipitalis transversus is quite apparent. At first sight the outer limb of the latter sulcus appears to be continuous with the sulcus praelunatus; such is not the case, however, for they are separated by a narrow submerged gyrus. This point is important, for the normal relation of the outer limb of the sulcus occipitalis transversus is to lie between the sulcus praelunatus posteriorly and the sulcus occipitalis anterior anteriorly (fig. 7).

It will be seen from the description of the series of brains in this paper that the sulcus lunatus commonly exists in one or other of the forms described above. We are enabled, therefore, to make a classification of the occipital region for comparative anthropological purposes. This classification is based on the form and relations of two sulci—the occipitalis transversus and the lunatus.

Group 1 A comprises those specimens in which the sulcus lunatus proper is continuous with the pars medialis sulci lunati as a fully curved opercular sulcus; and in which the sulcus occipitalis transversus is completely buried on the anterior wall of the fossa lunata (fig. 2).

Group 1 B comprises those specimens in which the pars medialis sulci lunati is separated from the sulcus lunatus proper, revealing the "pli de passage supérieur"; and in which the sulcus occipitalis transversus is completely buried (figs. 6 and 7, *S.O.T.*).

I have seen six cases belonging to Group 1, in approximately 400 brains.

One does not find an abrupt change from the condition in which the sulcus occipitalis is buried to that in which it lies completely free anterior to the sulcus lunatus. As would be expected, the sulcus occipitalis transversus has a tendency to lag behind on the anterior wall of the fossa. Elliot Smith (10) (figs. 2 and 4) depicts one case in which the outer limb is overlapped by the operculum and one in which the inner limb is overlapped. In the Chinese it is more often the outer limb which is overlapped and this overlapping always takes place in the area of the sulcus lunatus proper (figs. 8, 9, 10 and 11).

The inner limb is not so frequently found on the anterior wall of the fossa and, when it is hidden, one almost invariably finds that it is to the pars mesialis sulcus lunatus that it is attached (figs. 12 and 14).

I propose to institute two groups for these types, to conform with the grouping of the completely buried forms.

Group 2 A comprises those forms in which the sulcus lunatus is complete, and in which the outer limb of the sulcus occipitalis transversus is on the anterior wall of the fossa. *Group* 2 B comprises the forms in which the pars mesialis sulcus lunatus is separate—in other words the "pli de passage

supérieur" comes to the surface, and the outer limb is joined to the sulcus lunatus proper.

Groups 3 A *and* 3 B differ from Groups 2 A and 2 B in that it is the inner limb of the sulcus occipitalis transversus which is covered (figs. 12 and 14).

In fig. 12 (brain 126) we see an example of the type included in Group 3 B. The apparent backward extension of the sulcus occipitalis transversus is explained. Davidson Black, in a note on the sulcus lunatus in man, says:

> On the right side (fig. 3) the caudal end of the interparietal sulcus (*B.N.A.*) is joined to a furrow which passes in a sagittal direction behind the mesial edge of the sulcus lunatus. In other words, the sulcus occipitalis transversus does not lie wholly in front of the lunate sulcus as is usually the case.

I have quoted this in full as it is of importance to appreciate the fact that the sulcus occipitalis transversus always does lie anterior to the sulcus lunatus. In the specimen depicted by Blake, the sulcus which he regards as the sulcus occipitalis transversus is the pars medialis sulci lunati, which is joined to the inner limb of the sulcus occipitalis transversus. It is a specimen belonging to Group 3 B.

The remaining types of occipital lobe have the one feature in common, that the sulcus occipitalis transversus is separated from the sulcus lunatus by a transverse gyrus of variable width. Two groups are to be recognised—firstly, *Group* 4, in which the sulcus lunatus is readily distinguishable, either in a complete form as in Groups 1 A, 2 A and 3 A forming the *Group* 4 A; or in which the pars medialis is a separate element with the exposed "pli de passage supérieur"—*Group* 4 B; and secondly, *Group* 5, in which the identity of the sulcus lunatus is not readily recognisable.

It is unnecessary to add anything to what Elliot Smith has already written on the form and relations of the type belonging to Group 4 A. It is desirable, however, to reproduce, for purposes of record, some typical examples of this group (figs. 13, 15*a*, 16, 17, 18, 20*a*, 20*b*, 21*a*, 22*b*, 23*a* and 23*b*).

Group 4 B likewise requires no description. It is illustrated in figs. 15*b*, 21*b*, 24, 25*b*, 26 and 27.

Group 5. In many cases the pattern of the lateral occipital region closely approximates to the pattern shown in European text-books, that is, the identity of the sulcus lunatus is obscured. The series of brains which I have had the opportunity of examining is so complete in all its stages that the homologies of the sulci are revealed, and the ape-like forms can be harmonised with these forms in which no occipital operculum is present. Before describing these stages, however, it is necessary to fix and homologise the more constant and conspicuous landmarks. These landmarks are closely related to the system of sulci which have arisen from the parallel sulcus, so that the inclusion of some of the sulci in the inferior parietal lobule is necessary.

The first sulcus to be considered, on account of its constancy in the brain of the Chinese and the anthropoids, is the sulcus praelunatus. This important landmark acts as an almost infallible guide to the sulci on the lateral surface.

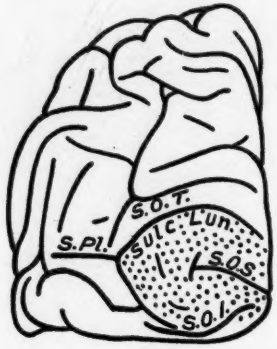


Fig. 16.

Fig. 17.

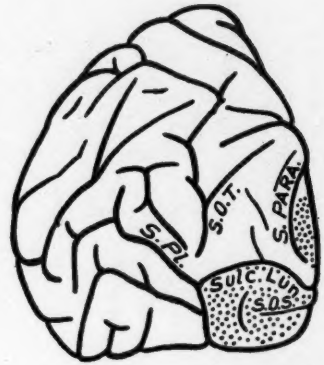


Fig. 18.

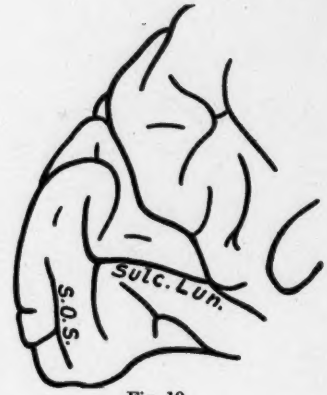


Fig. 19.

Fig. 20*a*.

Fig. 20*b*.

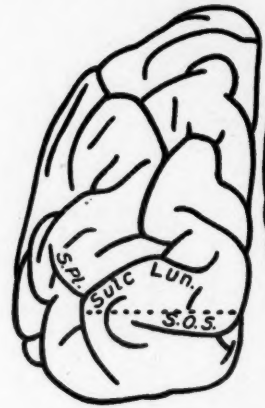


Fig. 21*a*.

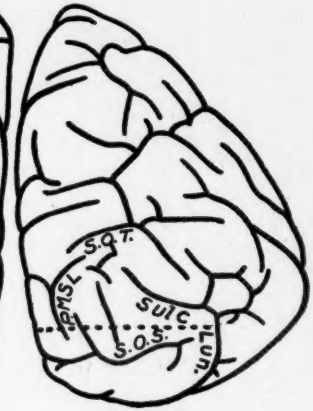


Fig. 21*b*.

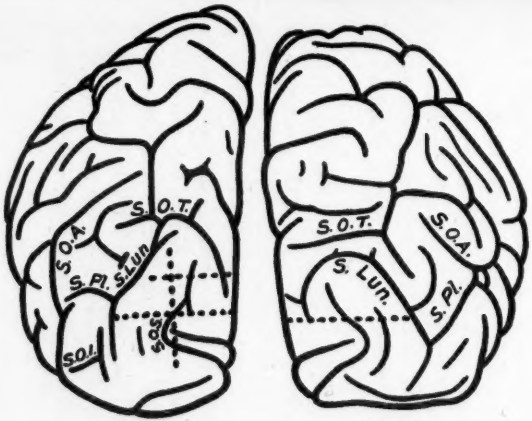


Fig. 22*a*.

Fig. 22*b*.

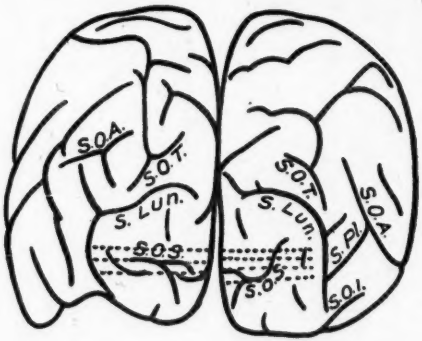


Fig. 23*a*.

Fig. 23*b*.

Fig. 24.

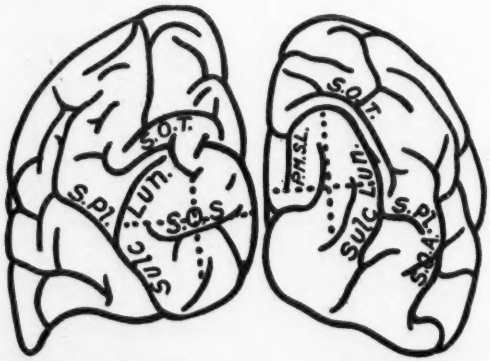


Fig. 25*a*.

Fig. 25*b*.

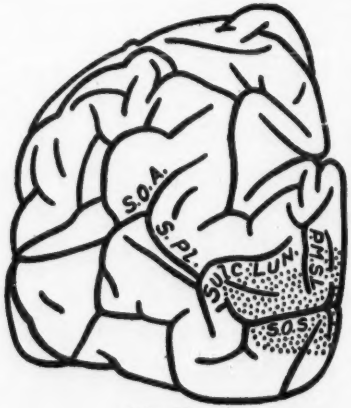


Fig. 26.

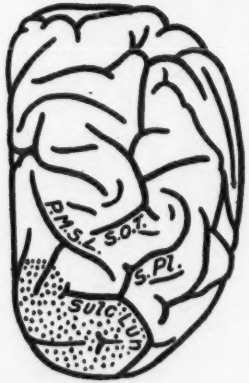


Fig. 27.

Elliot Smith(1) first refers to it in the Egyptian brain, and there appreciated the fact (p. 82) that the so-called lateral occipital sulcus of other anatomists is in reality a composite sulcus formed by a horizontal sulcus lunatus and the sulcus praelunatus. Although his evidence for this was not altogether conclusive, the series of brains under consideration fully confirm his opinion. It is a fortunate circumstance that in many of the brains the horizontal sulcus lunatus limits the striate area (figs. 26, 28 and 30). In this series the complete evolution of the lateral occipital sulcus is seen. It is not therefore strictly accurate to designate the sulcus occipitalis lateralis either as the sulcus praelunatus or lunatus; and so, it would seem preferable to retain the old term of sulcus occipitalis lateralis, understanding thereby the composite sulcus. The "plis de passage" of Gratiolet now become apparent; one can harmonise the older, purely descriptive, terminology with that which takes into account the evolution and physiology of the region, and there exists no reason for denying the homology of the sulcus lunatus in accepting the presence of these "plis de passage."

The sulcus praelunatus passes anteriorly towards a vertical sulcus which is frequently described as the sulcus temporalis superior. This name gives a wrong impression of its identity. It is the sulcus occipitalis anterior (*S.O.A.*). The sulcus temporalis superior, if by that term is meant the homologue of the parallel sulcus, normally ends, in the apes, by arching over the Sylvian fissure. In Quain's *Anatomy*(14), fig. 288, p. 300, a picture of the left cerebral hemisphere of the chimpanzee is given. It shows, arising from the parallel sulcus, a vertical sulcus which is the sulcus in question. It arises in the angle formed by the sulcus occipitalis transversus and the sulcus paroccipitalis and passes directly downwards to the tentorial border, to come into close relationship with the sulcus occipitalis inferior; in fact it is frequently joined to it. It is to this vertical sulcus that the sulcus praelunatus may become attached. In the Chinese, the sulcus occipitalis anterior is sometimes a separate element from the sulcus temporalis superior. When it is joined therewith, it is joined by means of a short connecting piece in common with the sulcus angularis—a sulcus which Elliot Smith has shown to be distinct in its origin from the sulcus temporalis superior. The form and relations of the sulcus occipitalis anterior are shown in figs. 1, 2, 6, 8, 9, 10, 11, etc.

The sulcus occipitalis inferior (*S.O.I.*), although subject to considerable variability, is another important landmark, and in all probability is represented in all human brains. In the Chinese it is found very frequently in the same form as one sees it in the apes. In the gibbon, it is a horizontal sulcus lying along the tentorial border, extending from the concavity of the sulcus lunatus to the second temporal convolution. In the Chinese this form is frequently present (figs. 10 and 22*b*). In the higher apes (fig. 1) it assumes a T-shaped form. The upper limb of the T lies parallel with the lower end of the sulcus lunatus. The stem of the T arches forwards under the tentorial border, to appear again on the lateral surface and join the sulcus occipitalis

anterior (figs. 6, 8 and 26). The junction of the stroke of the T with the stem is, however, more commonly on the inferior surface, and the sulcus may become connected with the sulcus collateralis.

I have nothing to add to what Elliot Smith has written on the sulcus occipitalis superior. It is found in a great variety of forms, from the primitive

Fig. 28.

Fig. 29.

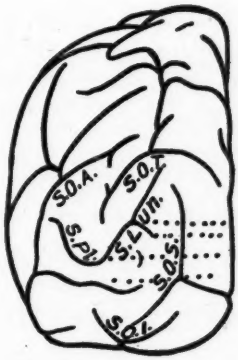


Fig. 30.

Fig. 31

condition seen in fig. 19 to the condition in which it is represented by rudimentary sulci.

It will be observed from the illustrations that, in the majority of specimens, the extent of the line of Gennari has been determined. In the Chinese, the lunate operculum definitely limits the striate area in a much larger percentage of cases than in other races so far described. In fully 75 per cent. of

cases it accurately delimits this area. Furthermore, the striate cortex is found in the great majority of specimens to extend for a considerable distance on to the lateral surface of the hemisphere.

GENERAL CONSIDERATIONS

The occipital region of the Chinese brain conforms to a type that reveals very clearly its agreement with a more primitive anthropoid type. The occipital region is similar in almost every respect to that of the higher apes, having a clearly marked sulcus lunatus extending well out on to the lateral surface of the brain, and, associated with it, are the paramesial, praelunate and transverse occipital sulci arranged in almost constant pattern.

Such variations as do occur are readily explicable. Our minds are hereby attracted to the significance of the brain as an organ of paramount importance in the interpretation of evolutionary problems.

The simple fact that the sulcus occipitalis transversus is overlapped by the operculum in the Anthropoid Apes and not in man has been unduly magnified as a distinctive feature. Those writers who, for this reason, would compare the brain of man directly with that of the Cebidae, thereby sacrifice the obvious means of explaining the presence of the paramesial and numerous other features in the occipital region, which are so clearly illuminated by a direct comparison with the Gorilla's brain (Elliot Smith on the brain of the Egyptian (1), (4), (5)).

The almost uniform arrangement of the sulci should also be of use in interpreting the more highly developed (perhaps specialised) brain of the European, and, no doubt, as further information of a functional character comes to hand, the meaning of a race retaining such primitive characteristics will become more and more apparent.

GENERAL SUMMARY

1. The brain of the Chinese shows that the sulcus occipitalis lunatus is normally present in its primitive condition. In the majority of cases, its posterior lip forms an operculum, and the stria of Gennari extends to the posterior lip of the sulcus.

2. The brain of the Chinese appears to be even more primitive, *i.e.* more directly comparable with the anthropoid brain, in the occipital region than the Egyptian. This is corroborated by the fact that the sulcus occipitalis transversus is to be found in many cases within the lunate fossa.

3. The constancy of the sulcus lunatus and its attendant sulci permits of a clearer definition of the sulci in the parietal region. The sulcus occipitalis anterior is recognised more definitely than heretofore.

ABBREVIATIONS IN FIGURES

(*For Description of Figures see Text.*)

S. Lun.	Sulcus lunatus occipitalis.	*S. Para.*	Sulcus paramesialis.
S. Paro.	„ paroccipitalis.	*S.O.T.*	„ occipitalis transversus.
S.Pl.	„ praelunatus.	*P.M.S.L.*	Pars mesialis sulcus lunatus.
S.O.S.	„ occipitalis superior.	*S. Ang.*	Sulcus angularis.
S.O.I.	„ „ inferior.	*Sulc. Calc.*	„ calcarinus.
S.O.A.	„ „ anterior.		

Dotted areas indicate extent of area striata.

BIBLIOGRAPHY

(1) Elliot Smith, G. (1903). "The so-called 'Affenspalte' in the human (Egyptian) brain." *Anat. Anz.* Bd. xxiv, 83.

(2) —— (1903). "Note on the so-called 'Transitory Fissures' of the Human Brain." *Ibid.* 216.

(3) —— (1904). "The morphology of the retrocalcarine region of the cortex cerebri." *Proc. Roy. Soc.* vol. clxxiii, 62.

(4) —— (1904). "Studies in the Morphology of the Human Brain." *Records of the Egyptian Government School of Medicine*, vol. ii.

(5) —— (1904). "The Morphology of the Occipital Region of the Cerebral Hemisphere in Man and the Apes." *Anat. Anz.* Bd. xxiv, 436.

(6) —— (1907). "New Studies on the Folding of the Visual Cortex and the Significance of the Occipital Sulci in the Human Brain." *Journ. of Anat. and Physiol.* vol. xli, 198.

(7) —— (1907). "A new Topographical Survey of the Human Cerebral Cortex." *Ibid.* 257.

(8) —— (1911). "Le Cerveau d'un Tasmanien." *Bull. et Mém. de la Soc. d'Anthropologie de Paris*, p. 442.

(9) —— (1924). *Essays on the evolution of man*, p. 32.

(10) Pol, D. Hulshoff (1917). "The ape fissure—sulcus lunatus in Man." *Proc. Sect. Sci. Acad. Amsterdam*, vol. xix, 219 and 224.

(11) —— (1917). "The relation of the plis de passage of Gratiolet to the ape fissure." *Ibid.* vol. xix, 106–109.

(12) Retzius, G. (1896). *Das Menschenhirn*, Pl. XLV.

(13) Black, Davidson (1915). "A note on the sulcus lunatus in man." *Journ. Comp. Neur.* vol. xxv, No. 2. 132.

(14) Quain (1909). *Anatomy*, iii, Neurology, p. 300.

(15) Head, Henry (1923). "Speech and Cerebral Localisation." *Brain*, vol. lvi, part iv, 429.

[Note. Professor Shellshear was unable to get access to the memoirs on the Chinese brain recently published in Europe. Of these the extensive monograph by Professor E. Kurz, "Das Chinesengehirn" (*Zeitsch. f. d. Gesamte Anatomie*, Bd. lxxii, Abt. 1, 1924) calls for special mention as a work filled with a mass of detail that leaves the problem discussed by Shellshear in a somewhat nebulous state. G. E. S.]

THE FACIAL MUSCULATURE OF THE AUSTRALIAN ABORIGINAL

PART I

By A. N. BURKITT, M.B., B.Sc.
Challis Professor of Anatomy, University of Sydney,
and G. S. LIGHTOLLER, M.D.

The following work upon the facial musculature of the Australian aboriginal is based upon the careful dissection by one of us (G. S. L.) of two aboriginal heads, henceforth referred to as H. B. 1 and D. B. 2. The following data are available concerning these two aboriginals. H. B. 1 was an inmate of the Mental Hospital, Gladesville, Sydney, since 1920, suffering from General Paralysis of the Insane (Wassermann reaction positive). He was born at South Murwillumbah, N.S.W. As far as can be ascertained he was a full-blooded aboriginal. D. B. 2, born in Cobar, N.S.W. and was a full-blooded aboriginal. This was confirmed by the typical ornamental scarring of the skin of the chest wall.

Accurate anthropometric measurements have been taken of both heads, as well as thickness measurements of soft parts over recognised landmarks. These are described in the *Journal of Anatomy*, vol. LVII, Part 4, July 1923, where also a post-mortem photograph and figures of the nasal skeleton of H. B. 1 are given. Both men had lived under civilised conditions within recent years, and were somewhere between 40 and 60 years of age.

The nomenclature of this article is based upon dissection of European adult and foetal heads, as well as upon an analysis of slow motion pictures of the facial muscles in a European female suffering from lipodystrophia progressiva. These studies were carried out and described elsewhere by one of us (G. S. L.). The subcutaneous fat of the face in the above case was so reduced that the majority of the muscles could clearly be seen beneath the skin, when in action.

The nomenclature and order of description are based upon the following table:

I. *Platysma:*
- (1) Nape platysma.
- (2) Neck platysma.
  - (*a*) Pars aberrans (Ascendens vel transversus).
  - (*b*) Pars labialis.
    - (*a'*) Portio modiolaris and pseudo caput buccale (if present).
    - (*b'*) Portio labralis. [*See note on p.* 39.]
    - (*c'*) Portio mandibularis.

II. *Musculi nasi:*
- M. nasalis.
  - (*a*) Pars transversa and M. anomalus maxillae.
  - (*b*) Pars alaris.
- M. alaris.
- M. apicis nasi.

III. *Musculi circum orem:*

- A. Musculi quadrati labii:
  - (1) M. quadratus labii inferioris.
  - (2) M. quadratus labii superioris.
    - (*a*) Caput angulare.
    - (*b*) Caput infraorbitale.
    - (*c*) Caput zygomaticum.
- B. Modiolus et Musculi modioli:
  - (1) Musculi cruciati.
    - (*a*) M. zygomaticus and pseudo caput buccale (if present).
    - (*b*) M. caninus.
    - (*c*) M. triangularis.
      - (*a'*) Caput buccale ("risorius" of Santorini).
      - (*b'*) Caput latum.
        Caput transversum.
      - (*c'*) Caput longum.
  - (2) Musculi transversi:
    - (*a*) M. buccinator.
    - (*b*) M. orbicularis oris.
      - (*a'*) Pars marginalis.
      - (*b'*) Pars peripheralis.
      - (*c'*) Pars nasalis (septalis).
- C. Musculi accessorii:
  - (1) M. incisivus superioris.
  - (2) M. mentalis.
  - (3) M. incisivus inferioris.

IV. *Musculi circum oculum:*

- (1) M. orbicularis oculi.
  - (*a*) Pars peripheralis (M. malaris).
  - (*b*) Pars orbitalis.
  - (*c*) Pars palpebralis.
- (2) M. depressor capitis supercilii.
- (3) M. corrugator supercilii.
- (4) M. procerus.
- (5) M. frontalis.
- (6) M. transversus glabellae.

V. *Galea aponeurotica.*

VI. *Musculi post et circum aurem:*

- (1) M. occipitalis.
- (2) M. auricularis posterior.
- (3) M. auricularis superior.
- (4) M. auricularis anterior.
- (5) M. transversus nuchae.
- (6) M. auriculo-orbitalis.
- (7) M. auricularis inferior.
- (8) M. stylo-auricularis.
- (9) Intrinsic muscles of the ear.

This table will be seen to differ from most current descriptions, in the following features:

I. In considering the platysma—any fibres which previous writers have called "platysma risorius," are now classified as a pseudo caput buccale of the platysma. The zygomaticus risorius has been treated similarly.

The different types of platysma may be grouped as follows (after Bluntschli):

A. Absence of platysma.

B. Fibres of platysma have a general *transverse* direction.

(1) Well developed pars labialis and pars aberrans. Type I (Bluntschli).

(2) Well developed pars labialis but weakly developed pars aberrans.
Type IV (Bluntschli).

(3) Weakly developed pars labialis and absence of pars aberrans.
Type VI (Bluntschli).

C. Fibres of platysma have a general *vertical* direction.

(1) Well developed pars labialis and pars aberrans.

(*a*) Pars aberrans reaches above ear-mouth line.
Type II (Bluntschli).

(*b*) Pars aberrans does not reach above ear-mouth line.
Type V (Bluntschli).

(2) Well developed pars labialis and poorly developed pars aberrans.
Type III (Bluntschli).

Here the cranial portion of the pars aberrans fibres usually turn oralwards.

(3) Weakly developed pars labialis and absence of pars aberrans.
Type VI (Bluntschli).

When the platysma is poorly developed it seems impossible to determine to which type it belongs, hence Type VI of Bluntschli is shown as belonging to both groups.

Both from dissection and functionally the pars labialis fibres may be divided into three portions:

(1) The portio modiolaris, whose fibres enter the modiolus. Some of the uppermost fibres of this portion lie deep to the caput buccale M. triangularis ("risorius" of Santorini). In the absence of this latter muscle, these uppermost fibres may form a pseudo caput buccale (platysma risorius).

(2) Portio labralis, whose fibres enter the lower lip and reach to the red lip margin. These fibres cover the more lateral and deeper fibres of the M. quadratus labii inferioris, and may or may not be intimately blended with them. They do not, however, reach the median plane. Laterally they do not reach the angle of the mouth, leaving a very definite area of the lower lip not supplied by a labial tractor.

(3) Portio mandibularis comprises that portion of the muscle whose fibres are inserted into the basis mandibulae. Generally this is very broad, as many of its fibres underlie and are almost inseparable from the portio labralis.

II. This table also differs from current descriptions in the marked emphasis laid upon the modiolus ("node" of Quain, or "Knoten" of Eisler) as an area of origin or insertion for the facial muscles during speech and the consequent regrouping of the muscles around this.

III. The recognition of the fact that the M. triangularis of the current text-book descriptions is really composed of two sheets of muscle—one attached to bone (caput longum) and one not attached to bone (caput latum and transversum).

IV. The term M. risorius has been abandoned, and this muscle has been considered as a third caput to the M. triangularis (caput buccale), inasmuch

as it has been shown by cinematographic studies that it is not seen in activity during laughter, but only if the laughter is forced or an attempt is made to repress laughter (see also Duchenne, Le Double, Tome I, p. 24). In the absence of this muscle, its function may be performed by fibres from the platysma, or even from the M. zygomaticus. These fibres have been called "pseudo caput buccale" and are included under their respective muscles of origin. (Compare Bluntschli and others who call these fibres, "platysma-risorius" and "zygomaticus-risorius.")

V. Owing to confusion the terms M. depressor septi and M. naso-labialis have been avoided. The term M. depressor septi is used by Spalteholz to indicate the median fibres of the pars alaris M. nasi, by Cunningham to denote those fibres of the M. orbicularis oris which are attached to the nasal septum, and Rauber-Kopsch includes both these sets of fibres under the above term. In this article, therefore, the median portion of the pars alaris M. nasi has received no special name, and fibres of the M. orbicularis oris attached to the nasal septum have been called the pars nasalis M. orbicularis oris. The term M. naso-labialis has been rejected owing to comparative anatomists calling a totally different muscle by this name.

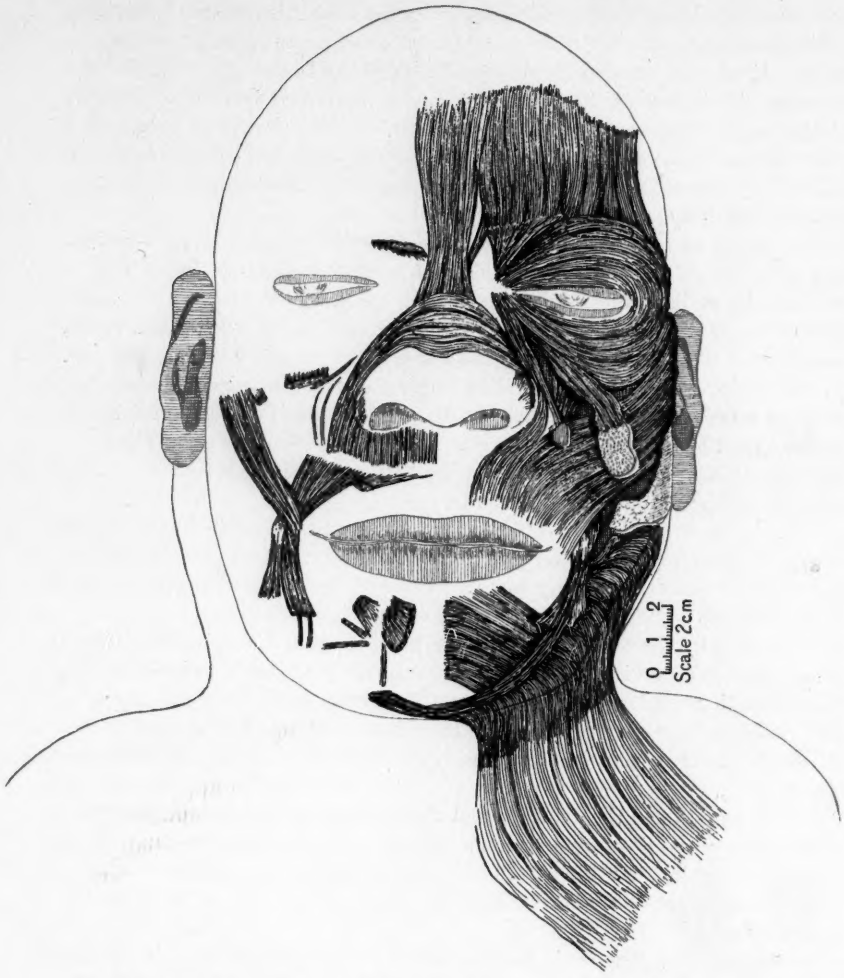
VI. As regards the M. orbicularis oris, cinematographic analysis and careful dissection have shown the arrangement and use of the pars marginalis in forming labial cords during speech, as hinted by Wilmart in *La Clinique*, Bruxelles, 1897, who called them "anches membraneuses."

VII. Finally the term pars peripheralis M. orbicularis oculi or M. malaris (Henle) has been revived to indicate a muscle layer lying superficial to the M. zygomaticus and caput zygomaticum M. levator labii superioris laterally, and medially lying superficial and lateral to the caput angulare of the M. levator labii superioris. This has been described and figured by Henle (1873).

We have retained the name M. malaris for conciseness, though apparently it comprises "reste" of two separate muscle complexes, the auriculo-labial complex laterally and the auriculo-orbito-fronto nasal complex medially. These two complexes are derivatives of the pars intermedia of the sphincter colli profundus (Huber).

Caput mediale. The auriculo-orbito-fronto nasal complex can be divided into an anterior and posterior portion—the anterior representing the M. naso-labialis (M. frontalis and M. procerus of man) and the posterior portion representing the anterior and superior ear muscles, and the M. orbito-auricularis (Huber). The caput mediale seems to represent, in part, at least, a survival of the more primitive condition of a M. naso-labialis, as found in lower mammals. Thus the primitive M. naso-labialis will be taken to be represented by the M. frontalis, M. procerus and caput mediale of the M. malaris. These remarks refer to that sheet of fibres lying superficial to the caput angulare.

Part of the medial head may be sharply differentiated to form a large muscle bundle ending in the cheek fat. This bundle was previously noted



Figs. 1 and 2 are pantographic tracings from photographs of the dissected head, corrected and amplified by direct measurements and observations.

Fig. 1. *Norma facialis, H. B.* 1. On the right-hand side the musculature as seen when the skin was first dissected off is figured, while the left-hand side shows chiefly muscle origins. In drawing these latter, the origin of the M. incisivus inferioris was placed too low down.

On the left-hand side of this figure many small muscular slips are depicted. These are as follows:

(1) Three slips of the M. anomalus maxillae lying between the M. nasalis and the origin of the caput infraorbitale.

(2) The two lateral slips of the caput longum M. triangularis are shown joining the deep surface of the terminal portion. These run almost vertically.

(3) Two aberrant slips belonging to the M. incisivus inferioris. The upper of these (which

should be more transverse in direction) is the M. premandibularis transversus (Eisler), and the lower was a slip joining the platysma.

(4) The M. anomalus menti is a slip shown running vertically below the M. mentalis.

Fig. 2. *Norma lateralis, H. B.* 1. The facial musculature as it appeared after the skin was removed. It will be observed in both figures how the sheet-like caput laterale M. malaris, the oculo-buccal portion of the caput mediale M. malaris, and the large development of the caput angulare of the superior labial tractor obscure from view the muscles usually seen in the middle region of the face, a small portion of the caput infraorbitale M. quadratus labii superioris alone being visible.

and described under the name M. oculo-buccalis (*Journal of Anatomy*, vol. LVII, part 4, 1923).

This bundle is probably an offshoot of the pars palpebralis M. orbicularis oculi.

The caput laterale comprises the orbito-labial portion and also some of the temporo-labial fibres of the auriculo-labialis superior of Lemurs (Ruge, 1886, p. 285). In the chimpanzee, a muscle sheet is present which consists of two portions—one with a superficial origin from the temporal fascia and the other with a deep origin from bone. The superficial corresponds to the caput laterale M. malaris and the deep to the M. zygomaticus (Virchow). In the orang, only the superficial layer corresponding to the caput laterale M. malaris is present and there is no true M. zygomaticus with a deep bony origin (Sullivan).

The great development of this sheet in the Australian aboriginal acting as a labial tractor gives more independence of movement to the outer portion of the lip than is found in the European and may be associated with the "grin" of the aboriginal.

The lip fibres of this complex are largely absent in the European and are replaced by subcutaneous fat.

THE FACIAL MUSCULATURE OF H. B. 1

In practically all cases in the head of this aboriginal, the symmetry was so well marked that no separate description was necessary for the right and left sides.

I. Platysma

(I) The muscle is poorly developed but forms a continuous sheet. The fibres are coarse and thick near the lower jaw, but weaker and thinner caudally. The coarse bundles extend laterally as far as a vertical line 2·1 cm. below the angle of the jaw and form a roughly triangular area beyond which the bundles are much thinner and paler (see fig. 2).

Cranially, the muscle is below the mouth-ear line. Caudally, the fibres reached to the clavicle.

The right fibres cross the left in the mid-line at the gnathion and for a distance of 1·4 cm. caudal to it. At the clavicle the sheets are separated by a wide interval of several centimetres.

(II) The muscle belongs to the Type III (Bluntschli) in which the pars aberrans fibres are weakly developed and whilst chiefly vertical turn oralwards at their cranial end.

The pars aberrans in this case, though weakly developed, ascended to be attached to or interlace with almost the whole of the caput buccale M. triangularis ("risorius" of Santorini) at an obtuse angle. Posteriorly, a sliver of the pars aberrans is attached to the fascia of the parotid gland in its lower portion and its most posterior edge crosses the sternomastoid muscle at a point 3·8 cm. vertically below the lobe of the ear.

Pars labialis. The portio modiolaris was normal. The portio labralis was well developed, 1·7 cm. broad, passing beneath the caput longum M. triangularis and when it met the underlying M. quadratus labii inferioris, the two sets of fibres were inseparable. The fibres of both muscles ran in the same direction. The more minute details of their insertion will be described elsewhere.

The portio mandibularis. As has already been mentioned, the fibres of the two sides interlaced at the middle line, and extended laterally to a point 1·4 cm. lateral to the foramen mentale. No nape platysma was present.

II. Musculi Nasi

M. nasalis. The pars transversa portion of the anomalus maxillae and the pars alaris formed a continuous sheet of muscle arising from the maxilla in the infra-nasal fossae, from the mid-line to a point above the centre of origin of the M. caninus (see fig. 4). The pars transversa was well developed and fleshy throughout and at the lateral edge of the cartilago alaris major was ·7 cm. broad and ·18 cm. thick. It spread out into a broad muscular sheet which joined its fellow of the opposite side, across the cartilaginous bridge of the nose. In the middle line it extended down almost to the apex of the nose. Above it interlaced intimately with the fibres of the M. procerus.

There is thus a continuous muscular covering from the glabella almost to the apex of the nose in the mid-line.

It will be seen that it lies between the alar cartilage and the upper and lateral margins of the bony aperture of the nose. It is thus a post-vestibular constrictor of the nasal airway (*vide* Burkitt and Lightoller, and Lightoller).

The pars alaris. The most medial fibres of this are often known as the M. depressor septi, but for reasons already given this term has been abandoned. It is a thick, well-developed muscle, whose medial fibres are covered by the pars nasalis M. orbicularis oris. It has the normal three insertions, into the septum mobile (septal cushion), into the lower margin of the nasal openings and the lateral margin of the ala nasi; these latter fibres were well marked.

The M. anomalus maxillae was present on both sides, being in each case represented by three fleshy bands, two of which, lateral to the pars transversa, are inserted into the periosteum of the maxilla medial to the infra-orbital foramen. The third fleshy band was represented by some fine muscular slips crossing the former almost at right angles. These were attached to the frontal process of the maxilla under the caput angulare and again to the maxilla under the caput infraorbitale of the M. quadratus labii superioris. Both these groups are classified by Eisler under the name of M. anomalus maxillae, though it is doubtful if they are of common origin.

The M. alaris was a thick solid sheet arising from the lateral crus of the alar cartilage and possibly from the region of the lateral bony margin and converging to the nostril. It was closely bound with connective tissue and difficult to dissect. No trace of a M. apicis nasi could be found.

III. Musculi circum Orem

(1) *M. quadratus labii inferioris.* The muscle is much more extensive and powerful than in the average European. The lateral fibres are inseparable from the portio labralis platysmae. The fibre bundles are very coarse.

The muscle forms a broad sheet extending from the red lip margin to the point of the chin and from the median plane to a vertical line through the 1st lower molar. The muscle sheet thins towards the middle line and the fibres interlace with those of the opposite side, without the formation of a raphe. The uppermost fibres interlace at an acute angle and the lowermost in a broad arc of apparently continuous fibres.

The insertion into the skin is more extensive than normal, covering the whole of the medial portion of the lower lip and the whole of the chin, medial to the origins of the two capita longa of the M. triangularis. Microscopically, the insertion showed the three sets of fibres already described by one of us.

The deeper fibres to the mucous membrane interlace with the fibres of the M. orbicularis oris in the median plane at a distance of 3·35 cm. from the rima oris and are, therefore, almost at the periphery of the orbicularis oris. More laterally the deeper fibres interlaced closer to the rima oris, thus following the outline of the margin of the M. orbicularis oris and are here only 1·5 cm. from the rima oris. The most lateral edge of the combined muscle sheet (M. q. labii inf. and portio labralis platysmae) is 1·0 cm. medial to the angle of the mouth.

Bony origin. This is of much greater extent than in white races. Posteriorly it is attached close to the fornix of the mucous membrane, as far back as and just below the 1st molar tooth and at this point is both posterior and superior to the foramen mentale. Here its fibres interdigitate with the origin of the anterior fibres of the lateral attachment of the M. triangularis (q.v.) for 0·6 cm. Extending downwards and forwards in a slightly curved direction it reaches to within ·45 cm. of the median plane and here again the fibres interdigitate with the origin of the M. triangularis. The total width of the muscle is 3·1 cm. The portion of the muscle uncovered by the labral platysma takes origin from the corpus mandibulae, along a line common to it and to the insertion of the portio mandibularis platysma.

The medial fibres of the M. quadratus labii inferioris, *i.e.* those fibres which interdigitate with the medial origin of the caput longum M. triangularis, are very thick and powerful (0·22 cm.). They are inserted into the skin of the chin below the sulcus mento-labialis.

The M. quadratus labii inferioris completely covers all the muscles of the chin and lower lip including the M. orbicularis oris, M. incisivus and M. mentalis. There is a slight interlacement of fibres with the M. incisivus inferioris, but very strongly marked interlacement with the M. orbicularis oris and the M. mentalis. Though a continuous sheet of muscle, the lateral and medial

halves must have quite different actions, the lateral half (in conjunction with the portio labralis platysmae) acting wholly upon the lip, and the medial half, which is equally strong, acting solely upon the chin below the sulcus mento-labialis.

(2) *M. quadratus labii superioris.* The muscle is particularly well developed as were the other muscles of the face. The fibre bundles are coarse. The muscle may be described as consisting of two portions, the three heads above and the common sheet below. Its breadth at the point where the three heads fuse and send fibres to the naso-labial fold is R. 1·5 cm., L. 1·76 cm., and its thickness 0·4 to 0·5 cm. The three heads fuse together at the level of the lower border of the nose and in the naso-labial sulcus.

A considerable mass of fibres turn into the skin of the furrow at a distance of 3·61 cm. from the mid-line. These fibres are chiefly derived from the angular head of the M. quad. l. sup., and from the lateral head of the M. malaris. The main body of fibres, however, continue forward deep to this to cover the whole of the upper lip in conjunction with the M. zygomaticus and lateral head of the M. malaris, as far as the red margin of the lip.

The fibres extend almost to the middle line, as a thick and definite sheet. From the naso-labial furrow down to the red margin of the lip, fibres are partly turning up into the skin and partly interlacing with M. orbicularis oris to reach the mucous membrane, so that the sheet which is thick and definite above becomes thin and ultimately disappears at the red margin of the lip. The deep surface of this common sheet at the level of the lower border of the nose interlaces with the M. incisivus superior in part.

In Eisleir's description of the muscle in the European, the muscular bellies end in the region of the naso-labial fold, but he definitely states there is a layer of tendinous fibres continuing on to the red lip margin. In contrast to this, in the aboriginal the muscular bellies themselves continue to the red lip margin. We have also found a similar condition in the European, but the muscle fibres are less well developed.

Further, in the head of a full time European foetus (Australian born European), the whole of the upper lip was found to be covered by this muscle sheet, exactly as in the adult aboriginal.

The above accounts differ from the description current in English text-books (Cunningham, Gray, Morris) and also differ from Virchow's account.

Caput angulare. This arises from a narrow linear area running obliquely along the frontal process of the maxilla. Its upper end is ·75 cm. from the mid-line and 0·2–0·3 cm. above the medial palpebral commissure. Its lower end is 2·42 cm. from the middle line, while the total length of origin is 2·62 cm. The origin runs parallel and immediately antero-medial to that of the oculo-buccal muscle, a portion of the medial head of the M. malaris. The total length of the muscle to the point where fibres enter the skin of the naso-labial furrow is 5·1 cm. At the level of the pars transversa M. nasalis, it is 1·31 cm. broad and 0·11 cm. thick. Some bundles interlace with the pars transversa

at the upper limit of the naso-labial furrow and, passing beneath this, end in the ala nasi.

Those fibres of the common sheet (already described) which pass towards the philtrum seem to be chiefly derived from this head. The fibres lateral to these are seen to be inserted into the skin of the naso-labial furrow.

It receives no fibres from the M. procerus, frontalis, orbicularis oculi, or depressor capitis supercilii, nor did its origin run laterally into that of the caput infraorbitale. Its deep surface where it forms part of the common sheet interlaces with the M. incisivus superior.

In the description of the caput angulare are included the more medial fibres of the caput mediale M. malaris; their significance was not recognised at the time the head was dissected, as our attention was focussed solely on the M. oculo-buccalis, or more lateral fibres of this caput mediale M. malaris.

Caput infraorbitale. This muscle is thick and well developed but not very broad, being narrow and thick with coarse bundles. The muscle forms a sheet 2·18 cm. long from its origin to the first skin insertion. Its origin is 1·25 cm. broad and 0·45 cm. below the infraorbital margin, the centre of the muscle origin being immediately above the infraorbital foramen. There is a well-marked roughened area on the bone indicating the origin of the bulk of this muscle.

Its breadth equals 0·96 cm. just below the point of origin and its thickness is 0·22 cm. It spreads out fan-wise at the lip insertion. Portions of the fibres insert into the skin of the lip from the labial side of the naso-labial furrow as far as the red lip margin. The remainder of the fibres interlace with the M. orbicularis oris and incisivus superior (cf. microscopic sections).

Caput zygomaticum. This is the weakest of the three heads, though still coarse fibred. It is covered by a superficial layer of fibres belonging to the M. malaris (q.v.).

It arises from the bone at the inner end of the bony origin of the M. zygomaticus. It is a thin narrow band which partially fuses with portions of the M. malaris just before joining the caput infraorbitale. The remainder of this head pursues a curved course forwards and medially to join the caput infraorbitale just deep to and at the lower border of the oculo-buccal muscle—its length being 5·53 cm. from its bony origin to the common skin insertion below the naso-labial furrow. It and the infraorbital heads are partially concealed by the overlapping lower fibres of the orbicularis oculi and the M. malaris.

Its insertion is like that of the other heads.

The modiolus

This term was introduced in preference to the term "node" or "Knoten" of German writers, inasmuch as this area is not merely of anatomical interest, but is of prime importance functionally. It has been named after the Latin term for the "hub of a wheel," since the six chief muscles which enter into

its composition form the radiating spokes of an imaginary wheel—(the caput longum and caput latum M. triangularis are here considered as two separate muscles). A full description has been given elsewhere both for modioli of H. B. 1 and two European heads.

One striking feature of the modiolus in H. B. 1 is that the musculi cruciati form a Y- instead of an X-shaped muscle mass (see fig. 1). This was due to the vestigial condition of one limb of the X, the caput latum and the ribbon-like shape of the caput longum M. triangularis. At the modiolus, this Y-shaped mass is 1·7 cm. broad and 0·64 cm. thick.

Musculi modioli

(1) *Musculi cruciati modioli.*

(*a*) *M. zygomaticus.* The muscle is exceptionally large and powerful. The fibres were coarser than those seen in white races.

The length of the muscle was 7·12 cm. from the origin to the angle of the mouth. The breadth of the muscle was as much as 1·75 cm. and its thickness was 0·33 cm. The posterior border is thick, rounded, and sharply defined (0·9 cm. thick).

It belongs to Type I of Bluntschli. Its origin from the zygomatic bone was immediately above the ridge raised by the tendinous fibres of the M. masseter, being a transverse oval area 1·0 cm. long extending back to within 0·3 cm. of the zygomatico-temporal suture. The origin consisted of short tendinous fibres. The muscle is intimately blended with the caput laterale M. malaris.

Towards its insertion, the muscle is divided in the customary way, into superficial and deep portions, by the M. caninus. There is an intimate blending between this latter muscle and the superficial fibres of the M. zygomaticus. The insertion of the muscle into the modiolus has been fully described elsewhere.

The great size of the muscle is indicated by the fact that the whole of the superficial fibres pass anterior to the caninus and that the deep fibres have two large areas of insertion into the basis modioli and form the bigger of the two divisions. This is much more extensive than in the heads of Europeans so far examined.

(*b*) *M. caninus.* This muscle is broad, powerfully developed and coarse fibred. It forms a broad sheet at its origin (1·8 cm.) and just before it passes between the two heads of the M. zygomaticus it is 1·5 cm. broad and 0·2 cm. thick. Deep to this muscle and close to the angle of the mouth runs the arteria maxillaris externa in a "cellular" mass of fibrous tissue. The artery is often inaccurately represented as passing anterior to the M. caninus.

At its origin, it is in contact with the M. anomalus maxillae, the M. incisivus superior and the M. nasalis. As regards the bony origin, this extends in an oblique line 1·8 cm. long, from the lateral side of the canine ridge or jugum alveolare, upwards and outwards to a point 0·9 cm. inferior and a

little lateral to the infraorbital foramen. Its outer border is 1·2 cm. medial to the edge of the masseter muscle. Both the M. zygomaticus and the M. caninus are particularly well developed.

(*c*) *M. triangularis.* This muscle will be described under the following heads (cf. Introduction): (1) Caput longum, which in this subject forms the main mass of the muscle, (2) Caput latum and Caput transversum, and (3) Caput buccale.

1. Caput longum. On both sides this formed a thick, broad, fleshy band of coarse bundles 1·2 cm. to 1·5 cm. in breadth and 0·15 cm. thick near its origin to 0·18 cm. thick near the modiolus.

This fleshy band united intimately with the M. caninus and also with the M. zygomaticus to form the Y-shaped mass which in this subject represents the musculi cruciati modioli.

As a general impression it may be stated that the muscle is much larger and more powerful than is usually to be seen in the European. The distance of the lateral border from the middle line was 2·97 cm. The superficial insertion into the modiolus was much as usual, while the deep fibres attached to the basis modioli consisted of a small band entering the upper half of the basis which was derived from the deep central fibres of the muscle.

Bony attachment. This powerful caput has two points of attachment, a lateral and a medial, with a powerful bridge of muscle between, under which run the fibres of the portio labralis platysmae. The lateral origin was for two feebly developed muscle slips, while the median origin was for the main attachment of the caput.

(i) Laterally, a few posterior fibres take origin from the corpus of the mandible near the lower margin and vertically below the 1st and 2nd molar teeth. A few anterior fibres in this region also take origin from the bone at about the same level but vertically beneath the 2nd premolar tooth.

(ii) Medially, the main attachment of the muscle is an extremely powerful one extending from the middle line to the tuber mentale, a distance of 1·24 cm. At the middle line the muscle is 0·55 cm. broad and at the tuber mentale 0·94 cm. Some of the fibres seem to pass across the middle line thus giving the appearance of a continuous sheet of muscle beneath the chin.

From the extensive and unusual bony attachment the main body of fibres which form the caput longum runs more or less vertically upwards towards the modiolus forming a powerful muscular bridge under which the portio labralis platysmae fibres run to their insertion in the lower lip. This vertical direction is the direct result of the somewhat recessive chin and prognathic jaw of H. B. 1.

Again the peculiar attachment gives one the impression that a large caput transversum was present, but closer dissection showed that there was a very small caput transversum and a very unusual attachment of the caput longum to the protuberantia menti and even to the corpus mandibulae of the opposite side.

2. Caput latum and caput transversum. These formed a continuous fan-shaped sheet with (1) a few fibres anterior to the caput longum (M. triangulaire interne, Cruveilhier), (2) fibres lying superficial to the caput longum and extending beneath the chin across the median plane to form a sling stretching from modiolus to modiolus (caput transversum M. transversus menti), and (3) fibres lying lateral to the caput longum and arising from the fascia of the platysma. These three portions entered the modiolus, and could not be traced in detail.

3. Caput buccale (M. risorius). This muscle was poorly developed, consisting of thin curved bundles extending back 2·65 cm. to the middle of the cheek from the posterior border of the M. triangularis. Close to the modiolus its fibres run horizontally and at an angle to, not parallel with, the fibres of the platysma. More laterally, they curve upwards and are almost at right angles to the general direction of the platysma fibres.

For this reason they were not considered to be fibres of the platysma. Its insertion into the modiolus was not anterior to the remainder of the triangularis insertion. This might seem to indicate its being a platysma risorius, but there seems no adequate reason why the fibres of a triangularis risorius (or true caput buccale) should lie superficial to the main triangularis insertion. The fibres ended in the modiolus by interlacing with the other capita of this muscle.

(2) *Musculi transversi modioli.*

(*a*) *M. buccinator.* This muscle is large, powerful, coarse fibred and dark in colour, with the general direction of its fibres horizontal. The muscle is easily separated into three groups of fibres, upper, middle and lower, viz.:

(*a*) Upper. Those from the upper jaw.

(*b*) Middle. Those from the raphe pterygo mandibularis.

(*c*) Lower. Those from the lower jaw.

The point of junction of the upper and middle fibres is marked by the passage through the muscle of the duct of the parotid glands, otherwise, both these sets of fibres have little to distinguish them, as their general direction is very similar. The fibres of the upper group, it is true, have at first a downward inclination but they very soon run horizontally as do the fibres of the middle group.

The fibres of the lower group however (with the exception to be mentioned presently) wind obliquely around the lower fornix, and at first are directed obliquely upwards and but slightly forwards, later screwing once more around they adopt the general horizontal direction of the other fibres.

At first sight these fibres appear in their winding to cover over the middle group of fibres. This they actually do to a very small extent, and all three sets of fibres meet at the modiolus in practically the same plane.

They thus form a very definite pouch in the cheek which lies on the lateral surface of the mandible and is 1·5 cm. in depth, almost covering the mental foramen.

So though the distance between the origin from the maxilla and that from the mandible is only 3 cm. at its anterior end, the muscle is capable of considerable distension. No corresponding pouching was seen at the origin from the maxilla.

This distinction of three groups of fibres is lost anteriorly and the muscle consists of a continuous sheet of approximately horizontal fibres.

The length is difficult to estimate, but from the corner of the mouth to the centre of the pterygo-mandibular raphe is approximately 5·50 cm. The thickness of muscle + mucous membrane is 0·45 cm. The thickness of the muscle fibres is equal to 0·26 cm. (approx.). This dissection was difficult and some muscle fibres were removed with the mucous membranes owing to the intimate attachment of the two structures.

Attachments. The only attachment to the skin was a small and problematical one. A few of the lowest fibres arising from the mandible ran almost horizontally forwards, and passing under the caput longum M. triangularis ended between the fibres of the M. quadratus labii inferioris, and may have reached the skin. The whole of the inner surface is firmly and intimately bound to the mucous membrane of the cheek.

The attachment of the mucous membrane extends up to and includes the modiolar region. Posteriorly, the M. buccinator meets the internal and external pterygoid muscles upon the maxilla and the superior constrictor upon the pterygo-mandibular raphe. Anteriorly, by its insertion into the modiolus it is intimately connected with all the muscles attached to the region, viz. M. zygomaticus, caninus, triangularis, portio-modiolaris platysmae, orbicularis oris and incisivus inferioris, as well as with the M. quadratus labii inferioris. The modiolus is the main insertion of the muscle.

Bony origin. In the upper jaw this extended from a point opposite to the 2nd premolar tooth backwards to the hamulus. The fibres from the raphe are very few at its uppermost end near the hamulus, but large and numerous from the remainder of this fibrous band. The raphe itself is curved convexly forward and in fact the uppermost portion runs almost antero-posteriorly. The remainder of the origin takes place from the crista buccinatoria as far forward as the interval between the 2nd premolar and the 1st molar tooth.

The duct of the parotid gland pierced the muscle at the junction of the upper and middle fibres. This point was situated 4·0 cm. from the angle of the mouth, 1·1 cm. from the upper attachment of the muscle to the maxilla and 1·5 cm. anterior to the anterior border of the ramus of the mandible in the horizontal plane.

Two distinct groups of lymph glands were found on the superficial surface of the muscle at its anterior inferior extremity where it enters the modiolus. On the posterior superficial surface of the muscles was a considerable amount of fat (corpus adiposum buccae) and after this was removed about twelve small molar salivary glands were found.

(*b*) *M. orbicularis oris.* This muscle will be described in three portions—a

pars marginalis, underlying the red lip area, a pars peripheralis, or main body of the muscle, and a pars nasalis, attaching to the septum mobile nasi.

The muscle as a whole was larger and more coarse fibred than in the European, though its fibre bundles were not as coarse as those of the M. zygomaticus; also no difference in size was observed between the muscle fibres of the different portions. The pars marginalis and pars peripheralis formed the usual well-marked unciform muscle, as seen in a vertical section of the lip. The long arm of the hook (chiefly pars peripheralis) is 1·7 cm. in the upper lip, and 2·7 cm. in the lower lip. The short arm of the hook (pars marginalis only) is 0·7 cm. in the upper lip and 0·9 cm. in the lower lip. Near the middle line and 1·0 cm. from the lip margin, the pars peripheralis of the lower lip was 0·15 cm. thick. In the upper lip at a similar spot, the thickness was 0·12 cm. The greatest width across the hook was in the upper lip 0·4 cm. and in the lower, 0·55 cm. All these measurements were macroscopic and made on the dissected subject.

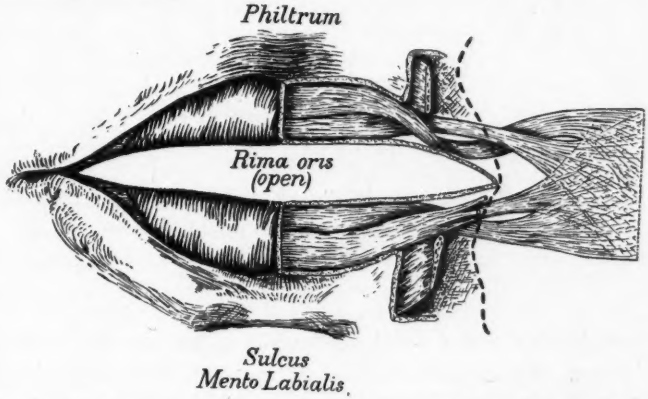


Fig. 3. This diagram indicates the arrangement of the fibres of the pars marginalis M. orbicularis oris in both upper and lower lips. Each pars marginalis consists of two well-marked bands, both of which laterally curl around the pars peripheralis to reach the deepest layer of the modiolus adjacent to the mucous membrane. The edge of the pars peripheralis is shown cut transversely in both lips. Notice also the small accessory slips of the pars marginalis inferior.

The relationship of these two portions of the M. orbicularis oris was the usual one; the whole of the pars marginalis curls around the pars peripheralis near the angle of the mouth, to reach that surface of the modiolus which lies nearest the mucous membrane.

Further, the pars marginalis itself is somewhat complex in the arrangement of its fibres, inasmuch as the fibres which are furthest from the rima oris in the median plane come to lie close to the rima at the angle of the mouth. It consists of two groups of fibres which twist completely round one another as they extend from the middle line to the modiolus. The more

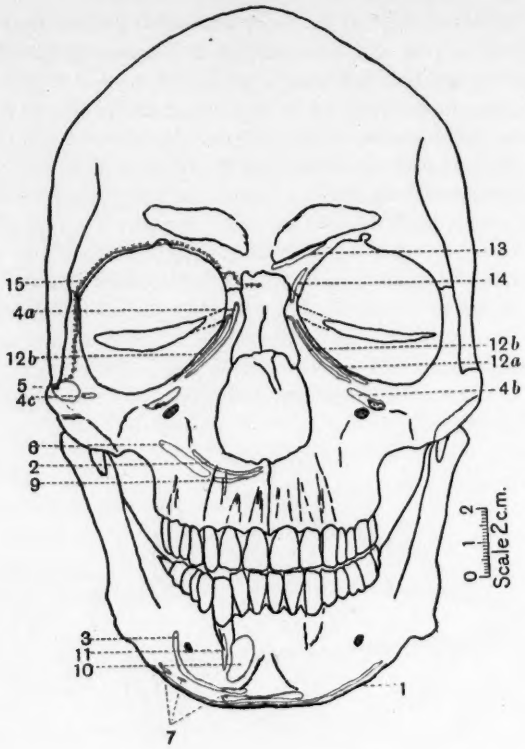


Fig. 4. *Norma facialis of skull of H. B.* 1. Muscle origins on Figs. 4 and 5 indicated as follows:

1. Platysma (portio mandibularis).
2. M. nasalis (pars transversa and pars alaris).
3. M. quadratus labii inferioris.
4 *a*. Caput angulare
4 *b*. Caput infraorbitale } M. quadratus labii superioris.
4 *c*. Caput zygomaticum
5. M. zygomaticus.
6. M. caninus.
7. Caput longum M. triangularis.
8. M. buccinator.
9. M. incisivus superioris.
10. M. mentalis.
11. M. incisivus inferioris.
12 *a*. Pars orbitalis
12 *b*. Pars oculobuccalis (*vide* M. malaris) } M. orbicularis oculi.
13. M. corrugator supercilii.
14. M. depressor capitis supercilii.
15. Galea aponeurotica (dot and cross outline).
16. M. occipitalis.
17. M. auricularis posterior.

elaborate twisting was seen in the upper lip, whereas the lower lip showed a mere crossing of its fibres (see fig. 3). This arrangement is somewhat different from that seen in Europeans.

Also it is to be noted that the fibres which are adjacent to the mucous membrane and therefore deepest in the modiolus are those which originally occupied the outermost portion of the red lip margin. Besides these two main bands which are found in both lips, in the lower lip two small muscle slips

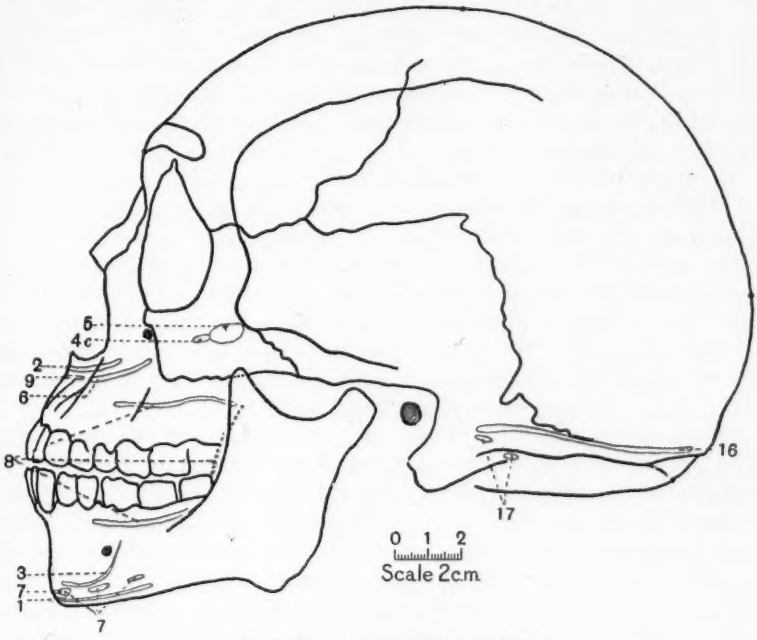


Fig. 5. *Norma lateralis of same skull.*

are found; one of these curves round the angle of the mouth to join the pars peripheralis of the upper lip just superior to the pars marginalis, while the other extends towards the mouth angle immediately beneath the skin and here helps to form a definite ridge (angulo-marginal ridge—see Lightoller).

The pars peripheralis was very similar to that of the European, except for its greater size and coarser fibres. No raphe was formed in the middle line in either the upper or lower lips, but a complete interlacement or continuation of fibres. On the deep surface of the pars peripheralis, the muscle presented in the median plane a rippled appearance, evidently due to this interlacement, whereas lateral to this, the muscle presented a perfectly smooth surface. In both lips anterior to the pars peripheralis, a central vein was present in the middle line.

The pars nasalis consisted of a well-developed set of muscle fibres forming a superficial and superior portion of the M. orbicularis oris. It was attached medially to the septum nasi mobile and posterior wall of the vestibulum nasi. Its lateral border is 1·9 cm. from the middle line.

C. *M. accessorii*

(1) *M. incisivus superioris.* Like the M. incisivus inferioris the muscle is well developed and its fibres equal to those of the M. orbicularis oris in size and pigmentation. At the canine eminence the muscle is 0·9 cm. in breadth and 0·14 cm. in thickness. Its origin is curved with the convexity downwards and extends from the middle line downwards and outwards as far as the origin of the M. caninus. It interlaces at its origin with the pars alaris and pars transversa M. nasalis.

At its origin it lies above and slightly posterior to the M. orbicularis oris. The fibres closest to this latter muscle come to lie on the same plane and intermingle with the fibres of the pars peripheralis and are inserted with them as they approach the angle of the mouth. The most lateral fibres however remain deeply situated and finally reach the superior cornu of the basis modioli by passing between the M. caninus and the deep portion of the M. zygomaticus. Like the M. incisivus inferioris, it takes origin above the fornix of the mucous membrane and passes over this to reach its destination. It is in contact with some mucous glands of the upper lip.

(2) *M. incisivus inferioris.* This is a well-developed sheet of muscle, being 3·0 cm. or more in length, 0·62 cm. in width and 0·15 cm. in thickness. Its fibres run in the same direction as, and are so closely applied to the lower margin of the M. orbicularis oris that, were it not for their origins, it would be difficult to differentiate these muscles. The fibres are much the same in size and colour as those of the M. orbicularis oris.

The muscle lies quite deep and close to the mucous membrane throughout its course. There are no attachments to the skin. The muscle runs laterally and slightly upwards from its origin to be inserted into the inferior cornu of the basis modioli and is thus brought in contact with the fibres from most of the modiolar muscles, including the M. buccinator. At the basis modioli the fibres are divided by a group of large mucous glands lying just below the angle of the mouth. Some fibres pass superior, but the majority inferior to these glands.

Quite separate from this main muscle belly and lying inferior to it are two separate muscular strands (see Fig. 1). One runs horizontally outwards for about 2·0 cm. to be again inserted into the bone (M. premandibularis transversus, Eisler). The other, about the same length and size, runs inferiorly and laterally towards the lower edge of the mandible, where it apparently joins with the portio labralis platysmae. These strands are not more than 0·25 cm. in width.

Origin. This is 1·13 cm. in width and is from the canine ridge, lying outside the fossula incisiva, and just lateral to the origin of the M. mentalis. The origin also lies immediately below the fornix of the mucous membrane, and the muscle crosses this obliquely to gain its insertion. With such a completely collapsible structure as the fornix, one can hardly apply the term "curling round." The muscle is in close contact with the mucous membrane as far as the mucous glands, near the angle of the mouth.

Though completely covered by the M. quadratus labii inferioris, it does not seem to be connected with it in any way.

(3) *M. mentalis.* This muscle like all the other facial muscles is better developed than in the European. The fibres are coarse and dark coloured. The large majority of fibres of the one side interlace with the fibres of the opposite side though many of the most lateral fibres enter the skin. This is especially true of the lower lateral fibres. In the present dissection the muscle seems divided into three portions:

1. The massive loops of muscle which take origin from the fossula incisiva between the jugum of the central incisor and that of the canine tooth. This area of origin measures 1·2 cm. in the vertical direction and 1·02 cm. in the horizontal plane. The two areas are 0·64 cm. apart and reach as far down as the upper margin of the tuber mentale, and lie immediately below the fornix mucosa of the lower lip.

The uppermost fibres are the shortest and run chiefly horizontally forming a solid mass of muscle 0·7 cm. thick vertically, and 0·95 cm. thick antero-posteriorly.

The lower fibres run with varying degrees of obliquity towards the chin and are also arranged in loops. But these loops now enclose between them a large mass of fibrous tissue which acts as the piston of the two cycle muscular cylinder (see Lightoller). The mass of fibrous tissue measures 1·7 cm. vertically and 0·55 cm. antero-posteriorly and 1·04 cm. (approx.) horizontally. The total vertical depth of this portion of the muscle is 2·6 cm. and the muscle sheet is 0·12 cm. thick. No raphe was present. Fibres from both of these portions of the muscle, besides decussating with each other, probably entered the skin on one or the other side of the middle line, but this was difficult to determine.

2. Fibres running parallel with and accompanying those lying lateral to the above-mentioned fibres. They arise from the lateral margin of the fossula incisiva and are inserted into the skin of the chin on either side of the middle line, but do not decussate or approach the middle line.

3. Anomalus menti fibres. These fibres are much weaker and paler than the rest of the muscle fibres hitherto considered. They arise from the bone immediately below the fossula incisiva and are there brought directly in contact with the lowest fibres of the incisivus inferior. These pale and weak fibres make no attempt to reach the skin but run along close to the periosteum to be inserted by a flat, shiny tendon into the lower portion of the tuber

mentale near the main insertion of the caput longum M. triangularis. The origin of all three portions was fleshy.

The muscle was not attached to the mucous membranes but the mucous membrane lies immediately above the uppermost area of origin. Its relation to the mento-labial furrow could not be measured.

There is a very close interlacement of the inferior fibres of the M. orbicularis oris and the superior fibres of the M. mentalis; so close, that they were quite inseparable and thus closed the top of the muscular cylinder.

Throughout the whole superficial surface of the muscle, its fibres are closely interlaced with the portio labralis platysmae and the M. quadratus labii inferioris. In the upper portion, therefore, we have the M. orbicularis oris, M. quadratus labii inferioris, portio labralis platysmae and M. mentalis, forming a close network of interwoven fibres. The origin from the bone was unusually large but fleshy throughout.

No fat cushion was encountered though a large fibrous pad filled in the gap between the lower muscular bellies.

A small and multiloculated ill-formed bursa lay between the tuber mentale and the fibrous pad.

The sulcus mento-labialis, like the naso-labial groove marks the abrupt transition from the fatty envelope of the face to the muscular snout region.

IV. Musculi circum Oculum

(1) *M. orbicularis oculi.*

This consists of three portions:

(*a*) *M. malaris* (*pars peripheralis M. orbicularis oculi*). Running from either edge of the M. orbicularis oculi and partially or wholly concealing the muscles of the mid-facial region (Lanz), there are two more or less complete but thin sheets of muscle fibres. These are the two heads of the M. malaris (capita mediale et laterale). As is usual, the caput laterale is partially overlapped by the caput mediale (see figs. 1 and 2).

Caput laterale. The fibres are coarser and the whole sheet thicker, more extensive and more closely united to the subjacent muscles (M. zygomaticus and caput zygomaticum), than is the case in the European. It is continuous with the outer edge of the pars orbitalis M. orbicularis oculi.

It is 0·1 cm. thick, 1·2 cm. wide and approximately 8 cm. in length. The fibres run downwards, forwards and medially to reach almost to the red lip margin, as is the case with the labial tractors. A few posterior fibres passed into the superficial area of the modiolus. The direction of its fibres is approximately parallel to that of the underlying muscles. It is chiefly owing to this broad sheet of muscle that the face of the Australian aboriginal, when dissected, presents such a muscular and unusual appearance.

Caput mediale. The more medial fibres lying superficial to the caput angulare were not noted as a separate sheet in this subject.

The more lateral fibres (or M. oculo-buccalis) arise from the frontal process

of the maxilla for 2·42 cm. along its orbital margin up to the medial palpebral commissure and also from the bone beneath the whole length of the commissure.

It lies in the upper margin of the naso-buccal gyrus (*Journal of Anatomy*, vol. LVII, 1923) and is inserted into the panniculus adiposus of the cheek about 2·46 cm. above and 2·0 cm. lateral to the angle of the mouth. The total length of the bundle is 6·65 cm. Its maximum width is 0·65 cm. and maximum thickness, 0·17 cm. Both this M. oculo-buccalis and the naso-buccal gyrus are well developed in the Australian aboriginal.

(*b*) *and* (*c*) *Pars orbitalis and Pars palpebralis.* These were large and well developed, being 0·1 cm. thick laterally. The following measurements were taken:

(N.B. In these measurements the word pupil is used to denote the centre of the pupil.)

(1) Pupil to upper margin	2·70 cm.
(1 *a*) Maximum upper breadth (1·4 cm. lateral to the pupil)	2·90 ,,
(2) Pupil to lateral margin	5·10 ,,
(3) Ectocanthion to lateral margin	3·25 ,,
(3 *a*) Bony orbital margin to lateral margin of muscle ...	2·70 ,,
(4) Pupil to inferior margin	2·30 ,,
(5) Pupil to medial margin	2·50 ,,
(6) Endocanthion to medial margin	1·0 ,,
(7) Pupil to ectocanthion	2·30 ,,
(8) Endo- to ectocanthion	3·70 ,,

In the horizontal measurements, the M. malaris has been included, whereas in the vertical measurements it has been excluded, as it could be differentiated below but not laterally.

The upper portion of the M. orbicularis oculi seemed to be moulded in relation to the bone; and ran from the medial palpebral commissure in a groove beneath the torus, and then expanded laterally as the torus disappeared.

The muscle was therefore expanded laterally and contracted medially, giving it a somewhat pear-shaped outline. This is possibly in correlation with the large torus and great width of the face in this region.

The torus was large and well marked (extending 3·48 cm. from the middle line) while the external angular process is 6·2 cm. from the middle line. Lateral to the torus, there is a shallow groove in the planum supraorbitale.

In the eyebrow region overlying the planum supraorbitale is an oval pad of fibrous tissue. This pad lies superficial to the pars orbitalis, but deep to the fine layer of the panniculus adiposus; from the latter it is quite distinct and is only loosely connected with it. This forms a movable torus lateralis and gives the overhang to the tail of the eyebrow.

The presence of the fibrous pad laterally and bony torus medially, give the eye a hooded appearance, very characteristic of the Australian aboriginal. Whether the overhanging eyebrow also observed in the white race is due to

similar causes has not been ascertained. The whole apparatus may act as a protection to bright sunlight, when required. Such a function has long ago been suggested for the bony torus (Darwin), but is probably purely secondary (Bolk, Burkitt and Hunter).

No sign of an external raphe was seen, nor any lateral bony attachment (see Sullivan).

Finally, the inferior bony origin of the pars orbitalis extended laterally to the medial end of the caput infraorbitale M. quadrati labii superioris (see fig. 4).

(2) *M. depressor capitis supercilii.*

This was a well-marked fan-shaped muscle, seen equally well on both sides. At the medial commissure it measures 0·5 cm. and at its widest portion, just below the torus, 1·27 cm., while it spreads laterally into the torus to a much wider extent.

It arose from the frontal process of the maxilla and the ligamentum palbebrale mediale, but no communicating fibres existed between it and the caput angulare M. quadratus labii superioris. Laterally it is in close connection with and difficult to separate from the M. orbicularis oculi. Our observations are not sufficient to determine whether the large size of the muscle and a large torus were correlated.

The vertical depth of its bony origin is 1·1 cm.

(3) *M. corrugator supercilii.*

This is a powerfully developed muscle, with an extensive and oblique bony origin from the nasal process of the frontal bone and the under surface of the torus, 1·9 cm. long. It passes obliquely upwards and laterally into the eyebrow at least 5·0 cm. lateral to the mid-line, thus extending well beyond the middle of the eyebrow. The width of its insertion into the eyebrow was 3·5 cm. in length. The thickness of the muscle was 0·1 cm. The fibre bundles were coarse.

(4) *M. procerus* (*M. depressor glabellae*).

This was a large well-developed muscle, directly continuous above with the medial fibres of the M. frontalis and joined the muscular pars transversa M. nasalis, 0·25 cm. above the lower ends of the nasal bones.

It was hourglass-shaped, its narrowest portion being opposite the commissure (0·9 cm.). The average thickness was 0·13 cm. On the left side, some deeper fibres of the M. frontalis joined the main muscle at a slight angle and passed beneath the most medial fibres of the M. depressor capitis supercilii.

(5) *M. frontalis.*

There was no gap in the middle line between the two halves of this muscle. The total width just above the eyebrows was 10·72 cm. while further back it spread out 13·22 cm.

Its greatest length from the glabella is almost 11 cm. Its thickness could not be estimated accurately, as the specimen was too dry.

Anteriorly, the muscle had no bony insertion, but either ran into the

M. procerus medially, or laterally into the skin of the eyebrow, after first interlacing with or piercing the M. depressor capitis supercilii, or orbicularis oculi.

V. Galea Aponeurotica

The galea aponeurotica which extends between the M. frontalis and M. occipitalis, was well developed, but apparently normal, so far as could be observed. What may be called the forehead galea ("Stirngalea," Eisler), which underlies the M. frontalis, extends beyond this muscle, to gain attachment to the bone as follows (see Fig. 4):

(1) In its inter-orbital portion it has a firm attachment to the nasal bones, immediately below the fronto-nasal suture, whence it runs obliquely upwards and laterally to the upper margin of the orbit. In this latter portion of its course, it is perforated by the fibres of the M. corrugator supercilii.

(2) In its orbital portion, it has an attachment to the bone in common with the septum orbitale (see Whitnall, p. 131). This bony attachment runs well beneath the torus or arcus superciliaris medially and the planum supraorbitale laterally, and extends down the outer margin of the orbit.

(3) From here it may be traced laterally, and transversely, across the malar bone, to which it is firmly attached. Behind this, it passes over the zygomatic arch, to become continuous with the deep fascia of the face.

It is interesting to note that the main division of the supraorbital nerve is running very obliquely on the left side. No observations were made on the right side (see Cunningham, 1907).

VI. Musculi post et circum Aurem

(1) *M. occipitalis.* This is a well-developed muscle, whose fibres run upwards and slightly laterally. Its medial edge at the occipital crest is 1·95 cm. from the middle line, 3 cm. above the crest, its medial edge is 2·55 cm. from the middle line.

The muscle fibres were not more developed than those usually seen in whites. The breadth of the muscle along the occipital crest is 6·35 cm. and the greatest length (about the centre of the muscle) is 4·25 cm. The muscle does not reach even approximately the pinna and is inserted over its whole length into the galea.

The thickness of the muscle sheet was 0·2 cm.

(2) *M. auricularis posterior* consisted of two narrow bellies, the superior being thicker but shorter than the inferior. They both arise from bone, the superior lying immediately anterior to the origin, and the inferior lying above the centre of the origin of the M. sterno-cleido-mastoid.

Both muscles are inserted directly into the eminentia concha, the upper being fleshy, with a very short tendinous insertion, whereas the lower has a long thin tendinous insertion.

(3) *M. auricularis superior.* This muscle was a large and well-defined fan-shaped muscle, with the usual attachments.

(4) *M. auricularis anterior.* This was represented by the most anterior fibres of the previous sheet of muscle.

SUMMARY

Facial musculature of H. B. 1

In general, the facial musculature was coarser fibred, darker in colour, and showed much greater development than is usually seen in the European.

We did not find any muscles which are not present in the European, though the concealment of the muscles of the middle region of the face by the greater development of the M. malaris (Henle) and the closer union of its caput laterale to the underlying muscles gave a very marked difference to the face when first dissected, and this was further emphasised by the remarkable development of a portion of its medial head (oculo-buccal muscle).

The greater development of the labial tractors, inasmuch as they obscured the M. orbicularis oris, further contributed to this appearance.

A well-marked fibrous pad underlying the outer portion of the eyebrow, and forming a movable torus, is a feature not hitherto described.

With regard to the individual muscles, the following features were worthy of note:

The *Platysma* was thick and dark in colour in the facial region, but weakly developed in the neck.

The *M. nasalis* was exceedingly well developed and muscular throughout; the pars transversa formed a very powerful post-vestibular nasal sphincter, as already mentioned (Burkitt and Lightoller).

The *two quadrate muscles* of the lower and upper lip were exceedingly well developed and had much larger origins from bone than are usually described. Their insertion was so wide that they covered the M. orbicularis oris as a thin sheet up to the red margin of the lip.

The Musculi quadrati labii inferioris completely covered the chin, forming a network with the underlying musculi mentales.

The *M. zygomaticus* was large and intimately bound with the overlying caput laterale M. malaris.

The *M. caninus* had a broad origin continuous with that of the M. incisivus superior.

The weak development of the caput latum M. triangularis resulted in the development of a Y rather than a X-shaped knot at the angle of the mouth. (Caput longum, M. triangularis, M. zygomaticus and M. caninus, see fig. 1.)

The *pars marginalis M. orbicularis oris* was peculiarly developed (fig. 3).

The *M. mentalis* was exceedingly large and powerful, with a large muscular origin, and a well-marked M. anomalus menti was present.

The *M. procerus* was well developed and its fleshy fibres were continuous with the pars transversa M. nasalis.

The *M. depressor capitis supercilii* was well developed.

The *frontal galea aponeurotica* was found not to be attached to the torus or planum supraorbitale and so could have no influence on the development of these bony eminences.

We wish to acknowledge our indebtedness to Professor E. Huber of the Anatomy Department, Johns Hopkins Medical School, Baltimore, for his classification of the facial muscles in Mammalia, as communicated to us in advance of publication and for help and advice; also, to the Anatomy Department, Sydney University, for the use of laboratories and material; to the late Professor Hunter and Acting-Professor Maguire; to Mr Louis Schaeffer and the staff of the Department, and to the Superintendents of the Gladesville Mental Hospital and Waterfall Sanatorium for particulars of the lives of these two aboriginals.

[When reading the proofs of Dr Lightoller's earlier memoir entitled Facial Muscles, published in this Journal, October, 1925, I was in some doubt as to whether the spelling of Dr Lightoller's new term *portio labralis* (p. 14) was intentional or not. Hence after consulting Professors J. T. Wilson and Sir Arthur Keith I altered it to "*labialis*." Dr Lightoller informs me that the new term was intentionally spelt "*labralis*."—G. Elliot Smith.]

BIBLIOGRAPHY

The following references have been added to those given in a previous communication. (Lightoller, 1925, This *Journ.*, Vol. LX.)

(1) v. d. Broek, A. J. P. (1920). "Über die Muskelinsertionen und Ursprünge am Unterkiefer; ein Bietrag zur Kinnfrage." *Zeitsch. f. Morphologie u. Anthropologie*, Bd. XXI.

(2) Cunningham, D. J. (1908). "The Evolution of the Eyebrow Region of the Forehead, etc." *Trans. Roy. Soc. Edinb.* vol. XLVI, part 2, 283–311.

(3) Fetzer, C. (1914). "Rassenanatomische Untersuchungenen 17 Hottentottenköpfen." *Zeitsch. fur Morphol. u. Anthrop.* Bd. XVI, Heft 1.

(4) Flower, W. H. and Murie, J. (1867). "Account of the dissection of a Bushwoman." *J. Anat. and Physiol.* vol. I, 189–208.

(5) Harslem-Riemschneider, L. (1921). "Die Gesichts muskulatur von 14 Papua und Melanesiern." *Zeitsch. f. Morphol. u. Anthrop.* Bd. XXII, Heft. 1, 1–44.

(6) Keibel and Mall (1910). *Manual of Human Embryology.*

(7) Popowsky, F. (1897). "Über einige Variationen der Gesichtsmuskeln beim Menschen und ihre Bedeutung für die Mimik." *Intern. Monatschr. f. Anat. u. Physiol.* Bd. XIV, S. 149.

(8) Ruge, G. (1887). *Untersuchungen über die Gesichtsmuskulatur der Primaten*, Leipzig, 1887.

(9) Seydel, O. (1892, 1894). "Über eine Variation der Platysma des Menschen." *Morphol. Jahrbuch*, Bd. XVIII and Bd. XXI.

(10) Sullivan, W. E. and Osgood, C. W. (1925). "The Facialis musculature of the Orang, Simia Satyrus." *Anat. Record*, vol. XXIX, No. 3, 195.

(11) Virchow, H. (1915). *Gesichtsmuskeln des Schimpansen*, Berlin, 1915.

(12) Whitnall, S. E. (1921). *The Anatomy of the Human Orbit and Accessory Organs of Vision.*

(13) Zeidler, H. F. B. (1914). "Beiträge zur Anthropologie der Herero." *Zeitsch. f. Morphol. u. Anthrop.* Bd. XVII, Heft. 2.

(14) ——. (1920). "Beiträge zur Anthrop. der Gesichtsweichteile der Neger." *Zeitsch. f. Morphol. u. Anthrop.* Bd. XXI.

OBSERVATIONS ON THE ANATOMY OF *HEXANCHUS CORINUS*

By CHAS. H. O'DONOGHUE, D.Sc., F.R.S.C.
(*Professor of Zoology, University of Manitoba*)

TOGETHER WITH

NOTE ON THE STRUCTURE OF THE LYMPHOID ORGAN (ORGAN OF LEYDIG) AND SPLEEN OF *HEXANCHUS CORINUS*

By LLOYD L. BOLTON

During the summer of 1925 a number of fresh dogfish, *Squalus sucklii*, and ratfish, *Hydrolagus* (*Chimaera*) *colliei*, were required for work in progress at the Biological Station, Nanaimo, British Columbia. For this reason a set line was put out fairly frequently, always yielding one or other of these forms. One day early in August the line was remarkably heavy and examination revealed the presence of a shark which had been caught on one of the hooks. It was too large to be hauled into the boat, so was towed ashore and, when landed, found to be a young female *Hexanchus corinus*.

The Elasmobranchs contain the most generalised of fishes and probably the most primitive and least specialised are the Notidanoids represented by the genera *Heptanchus* and *Hexanchus*. Fortunately the recent monograph on *Heptanchus maculatus* by Daniel(1) provides us with a large amount of information about this species of which the author says, p. 4, "Notwithstanding this lack of grace, I agree with Dean (1895) that '*Heptanchus* of all living sharks, inherits possibly to the greatest extent the features of its remote ancestors.'" No such information is available regarding *Hexanchus*, indeed, references to this genus are comparatively few and these are almost entirely to systematic works. No reference to the internal anatomy of *H. corinus* has been found. Jordan and Evermann ((8) p. 19) state that this species ranges from Monterey Bay, California, to Puget Sound, Washington, and it is not common. The present specimen, therefore, extends the range a good deal farther north and is the first definite record of its occurring in the seas of British Columbia. It is of interest on account of its comparative rarity and also as it is well over twice the length of the larger of the original specimens described by Jordan and Gilbert ((9), p. 352) which was only 43 inches long.

In view of the above facts, therefore, and in view of the importance of this genus from the morphological standpoint it was thought that the following observations would be of sufficient value to place on record. Unfortunately the conditions under which they were made—the animal was dissected almost entirely on the beach—excluded the possibility of even a moderately complete

examination of any one system investigated and no facilities were available for the preservation of such a large object entire. However, they do contribute something to our knowledge of this genus and additions may be made to them when opportunities arise.

The genus *Hexanchus* was founded in 1810 by Rafinesque (15) for the single species *H. griseus* and for 70 years this remained alone. In 1880, however, Jordan and Gilbert (9) described a second species, *H. corinus*, the shovel-nosed shark of the Pacific Coast of North America. The name is derived from corus or caurus, the north-west wind. One of the striking characters of the genus is pointed out by Daniel as follows: "Many of the Elasmobranchs are of the pentanchid type, that is those possessing five gill clefts, only *Chlamydoselachus* and those sharks belonging to the Notidanids exceeding this number. Record is also made of a greater number occasionally occurring in other forms. In *Chlamydoselachus* and in *Hexanchus* six clefts are present and in *Heptanchus*, as we have seen, there are seven, the greatest number known for any gnathostome or jaw-possessing vertebrate."

I desire to express my thanks to the Biological Board of Canada at whose station at Nanaimo these observations were made.

EXTERNAL CHARACTERS

Hexanchus corinus is somewhat similar in shape to *Squalus* or *Scyllium* but of a heavier build, with a relatively broader, blunter head and a much longer tail formed mainly of the elongated dorsal lobe although it is not nearly so extraordinarily developed as in the Thresher, *Alopias vulpes*. The colour of the whole fish was grey, dark grey above and lighter below but nowhere could it be considered black, the colour given by Jordan and Gilbert for their larger specimen, save in the mottling inside the lips.

Some of the important measurements of the fish may be given here for the sake of comparison with those provided by the last-named authors and it will be noted that the agreement is quite close. Fortunately the total length was such that the other measurements are practically percentages of this as they stand.

	inches
Total length from snout to tail	100·5
From snout to front end of dorsal fin	54·0
Length of base of dorsal fin	6·0
From hinder end of dorsal fin to base of tail	40·5
From snout to first gill slit	16·0
From first gill slit to last	5·0
From first gill slit to front end of pectoral fin	5·5
From hinder corner of eye to spiracle	5·0
From front of pectoral to front of pelvic fin	27·0
From end of ventral fin to tip of tail	32·0
Height of dorsal fin	6·5
Length of anterior edge of pectoral fin	11·5
Length of lateral edge of pectoral fin	3·5
Length of anterior edge of pelvic fin	5·5
Length of posterior edge of pelvic fin	7·5

Placoid scales are plentifully developed all over the skin. On the whole they are more tightly packed than in *Scyllium canicula* or *Heptanchus maculatus*; indeed if a small portion of the skin is examined it will be seen that the area of it occupied by the scales is noticeably greater than that free from them whereas in the second of the two forms just mentioned quite the reverse is the case. They are of two sizes, by far the greater number being small as compared with the actual size of the scales in *S. canicula* in spite of the far larger size of the species. They are arranged in more or less regular oblique rows with the free end of the blade directed backwards. In addition to these small scales there are others of the same type but with blades of more than double their area. These larger scales are not distributed generally but are to be found in irregular groups covering a square inch or so here and there on the body and head. Even with the naked eye this difference can be made out and the presence of the large scales is indicated by a coarseness in the pattern on the skin.

Each scale consists of a basal plate buried in the dermis, a neck and a blade exposed above the epidermis. The basal plate is approximately rhomboidal in shape with its sides slightly incurved so as to accentuate the angles; the anterior end of it projects well in front of the blade and bears two slightly raised narrow ridges. As a rule this blade is perforated near its centre by a moderate-sized hole leading to the pulp cavity but this may be replaced by two or three smaller ones. The neck is almost round but distinctly constricted. The blade lies almost at an angle of 45° to the basal plate and is also roughly rhomboidal. Its lateral and anterior angles are distinctly rounded while the posterior angle is distinctly though not sharply pointed. A strong, rounded ridge passes from the anterior angle backwards along the middle of the blade to near the hinder angle and a pair of similar but smaller ridges run backwards, one on each side near the lateral margins. The interior of the neck and blade is occupied by a large pulp cavity.

ALIMENTARY CANAL

The buccal cavity is furnished with numerous teeth as in Elasmobranchs in general but they are not present in so many successive rows as in many forms. There is no median tooth in the upper jaw. On each side of the middle line are two pairs of teeth one pair behind the other. The posterior pair on each side are in the line of the remaining teeth and the anterior teeth are about $\frac{3}{8}$ inch in front of this. All these teeth have a simple spine-shaped cusp with no subsidiary cusps or serrations or in some cases very minute serrations. Jordan and Gilbert state that there are six of these teeth or ten if another row, probably non-functional, are taken into account. The next three teeth on each side bear an anterior cusp, pointing upwards and slightly backwards with a single subsidiary cusp, directed almost horizontally at its lower posterior margin. The base of the main cusp is minutely serrated in front. The second tooth on the left side has two small cusps instead of one. Behind these the cusps increase to two or three instead of one. The succeeding five lateral teeth

diminish in size, the first cusp becomes smaller and the secondary cusps more upright so that there is a slight approach to the type of tooth in the lower jaw but the secondary cusps do not number more than three. Following these are seven very tiny teeth which likewise diminish in size as they pass backwards. Behind the row of teeth in use are two replacing rows with their blades pointing in the reverse direction to those in use. All the teeth of these rows are hidden by folds of mucous membrane except those of the seven posterior tiny teeth.

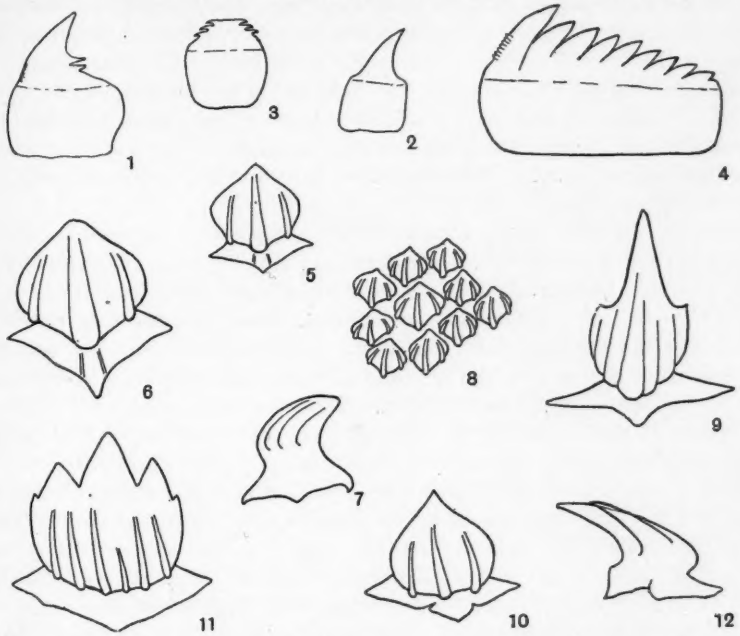


Fig. 1. Scales and Teeth of *Hexanchus corinus*. 1. Second of larger teeth on left side of the upper jaw. ×1½. 2. First of small anterior teeth in upper jaw. ×1½. 3. Median tooth of lower jaw showing lateral denticles. ×1½. 4. Second of the large teeth in the lower jaw. ×1½. 5. Ordinary dermal denticle of skin from above. ×32. 6. Large dermal denticle of skin from above. ×32. 7. Ordinary dermal denticle of skin from the side. 8. Group of ordinary dermal denticles *in situ*, blades only showing, to indicate arrangement. ×15. 9. Dermal denticle from skin of *Scyllium canicula* for comparison. ×32. 10. Medium sized stomodaeal denticle. ×32. 11. Large stomodaeal denticle. ×32. 12. Large stomodaeal denticle from the side. ×32.

The median tooth in the lower jaw is quite small with three tiny lateral cusps on each side. These lateral cusps are mentioned by Jordan and Gilbert (p. 352) but not by Jordan and Evermann ((8), p. 19). The lateral teeth are of large size as compared with the teeth in the upper jaw and of a different shape. There are six of them, the second and largest being about ⅞ inch long and the succeeding four diminish noticeably. The anterior spine on each tooth is much like that in the upper teeth save that it is distinctly serrated on its anterior

margin. It is followed by a line of seven or eight similar but smaller subsidiary cusps which arise from the base of the tooth and project upwards and not as in the upper teeth from the base of the first cusp and point backwards. Following this set of large teeth on each side is a row of five or six very small and degenerate ones. The replacing set of teeth lie behind the others and have their blades directed in exactly the opposite direction to those in use; only one set is visible.

It will be seen then that the teeth vary from those described in the type specimen particularly in the upper jaw where they appear to be somewhat simpler although, as already noted, the present specimen is of the same sex but more than twice the length of the type and so presumably older.

The teeth as a whole are very similar to those of *Heptanchus maculatus*, the most marked difference being the presence, in the latter form, of cusps on the anterior edge of the teeth of the lower jaw whereas we only find small serrations in *Hexanchus corinus*.

The buccal cavity in the Elasmobranchs being a stomodaeum is lined with ectoderm which has therefore the potentiality of bearing placoid scales. Often the only ones present are those developed in a highly modified form as teeth over the jaws but in certain forms like *Heptanchus*, *Heterodontus*, *Squatina*, *Alopias*, *Galeus*, *Mustelus*, etc. (*vide* Imms (7)) they may be present to a greater or less extent and in varying degrees of perfection. In the present species such stomodaeal scales are present in fair numbers towards the margins of both roof and floor of the buccal cavity. They are irregularly scattered and of various degrees of complexity. Some have simple blades only about a quarter the size of the dermal scales; others are much like the latter in size and shape and yet others larger and more complex. In all cases they are not so stoutly built, have relatively larger pulp cavities, the angle between blade and basal plate is only about 30° and the basal plate itself is thinner, often has notches in the edge and may be perforated by five or six holes. The largest ones are bigger than the larger dermal scales. Their blade possesses a strongly developed median point which may be flanked by two smaller points or cusps on each side and the raised supporting ridges while more slender may be increased to six in number. The presence of these stomodaeal denticles is a point of interest as are also their irregular distribution and range of variation.

The six gill pouches on each side open into the lateral and ventral walls of the pharynx by large slits which decrease in size as they pass backwards. The spiracle is a small opening externally and leads into the spiracular pouch. While the cavity of this is small compared with that of the other pouches it is relatively much larger than in forms like *Scyllium* and *Squalus* and opens into the pharynx by a moderate-sized internal cleft lying slightly more dorsal than those of the other gill pouches. This retention of a fair-sized spiracular pouch and internal opening is probably to be regarded as a primitive character. In correlation with its size we find its gill filaments are much more developed than in *Scyllium* and apparently resemble those of *Heptanchus*. The anterior

wall possesses twenty-five lamellar filaments which while smaller than those in the other pouches are nevertheless quite as well developed and beyond doubt functional. Thus we cannot speak of a pseudobranch but we have a definite though small spiracular hemibranch—another primitive feature. The posterior wall of the spiracular pouch is quite smooth and shows no sign of gill lamellae. It is coloured a deep grey which stands out in marked contrast to the surrounding yellow tissue or red gill filaments. The functional significance of this pigmentation, if any, is not obvious.

The anterior five of the ordinary gill pouches possess a very well-developed hemibranch on both front and hind walls. The anterior wall of the last gill pouch possesses a fully developed hemibranch and on its posterior wall is a small laterally situated hemibranch. This is about $1\frac{1}{4}$ inches long and consists of about twenty small but apparently normal lamellar filaments. From the examination of one specimen it is not possible to say whether this is always present but, if so, it is apparently unique, not being present in *Heptanchus maculatus*, in *Chlamydoselachus anguineus* nor in the typical pentanchid Elasmobranch.

A complete gill or holobranch is constituted by the skeletal, muscular and connective tissue in the partition between two pouches, constituting the gill bar, together with the hemibranch on the posterior wall of one pouch and that on the anterior wall of the succeeding one. Thus *Hexanchus corinus* possesses five complete gills and three additional hemibranchs, one on the front wall of the spiracle; the second on the front wall of the first or hyoidean pouch and the last on the posterior wall of the last pouch. This is one holobranch less and one hemibranch more than in *Heptanchus*, one hemibranch more than in *Chlamydoselachus* (in some specimens of this shark, however, the vestigial remains of a seventh arch but not cleft have been recorded, *vide* (6)), and one holobranch and one hemibranch more than in any other Elasmobranch. In addition, the spiracular hemibranch is functional and not a pseudobranch as in many forms.

From the above description of the gills it will be seen that apart from the large, broad, hyoidean bar between the spiracle and the hyoidean cleft, there will be five narrow gill bars showing on the inside of the pharynx. The first of these bears at its lateral angle two short, bluntly pointed, conical gill rakers; the second has two slightly larger with a sign of the third; the third and fourth bars bear three rakers and the fifth bar has three normal ones with a small fourth.

The oesophagus is a broad, flat, thick-walled tube much as in other Elasmobranchs but noteworthy because of the presence in its wall of a large, conspicuous, glandular body, the organ of Leydig which, while present in some species, is absent in many and not described in *Heptanchus maculatus*. The oesophagus passes over into the stomach without any noticeable alteration in dimensions although it is distinguished from that organ externally by its darker colour and greater apparent vascularity and internally by a totally different type of mucous membrane. The stomach, as in many Elasmobranchs,

is U-shaped. The proximal or cardiac limb is wide, about 13½ inches long, and attached to the mid-dorsal line along a large part of its length by the anterior part of the mesentery, the mesogaster. As it passes backwards it enlarges somewhat and becomes more bag-shaped and is produced into a sort of small, shallow diverticulum at its posterior end. Such a structure is apparently present in *Heptanchus maculatus*, for Daniel says (p. 125): "At the distal end of this part of the stomach (i.e. the cardiac part) there is a blind sac in which some of the folds terminate." This is not shown in his figures but a similar enlargement is clearly depicted by Woodland ((17), Pl. LVII, fig. 3) in *Centrophorus calceus*. The cardiac limb lies on the left side of the body cavity and in the present specimen was practically empty. The distal or pyloric lobe of the stomach is narrower and tubular and passes forward almost in the middle line for about 11 inches. It is attached to the cardiac end by a well-developed fenestrated omentum. The pyloric loop then bends over in a fairly wide curve and turns to run backwards. The lumen of this tubular portion of the stomach is very small but just at its termination it swells out and forms a distinct pyloric enlargement before finally and suddenly narrowing down to the pyloric constriction and valve. Such a terminal enlargement is also found in *Heptanchus maculatus*, for Daniel says (p. 126): "Three fourths of an inch from the termination of the pyloric limb there is a slightly enlarged portion which opens into the duodenum through the pyloric valve." Such a pyloric enlargement is present in various Elasmobranchs, e.g. *Scyllium* and *Squalus* and it may be quite well developed. Woodland says ((17), p. 869): "The pyloric portion of the stomach of *C(entrophorus) calceus* ends in a very short and small cul-de-sac, or, in other words, the duodenum or homologue of the bursa Entiana arises from the side of the pyloric region just before its termination."

The next region of the alimentary canal varies considerably in Elasmobranchs. To quote Daniel: "The part of the digestive tract immediately following the pylorus, the duodenum or middle intestine is well defined in *Heptanchus*. In figure 117, this segment (*du*) is covered in part by the ventral lobe of the pancreas (*pn.* 2). As in several other forms the valve of the spiral intestine extends forward throughout the length of the middle intestine and touches the pyloric valve." A comparison of fig. 117 with fig. 119 will show at a glance however that the part marked *du* in the former is not the duodenum at all but the enlargement at the pyloric end of the stomach. Further on (p. 138) we find the statement: "The duodenum may be encroached upon by the spiral valve through its entire course, as in *Heptanchus*, or it may be free as in a few of the sharks and rays." Now it seems to be a matter of opinion what is to be regarded as the duodenum. If we regard it as that part of the intestine immediately after the pyloric valve which contains no part of the spiral valve then *Heptanchus* like *Hexanchus* possesses no duodenum, while such a region is strongly marked in *Laemargus borealis*, *L. rostratus*, *Spinax niger*, *Centrophorus calceus*, *Chlamydoselachus anguineus* and *Hypnos subnigrum*. It is less well developed in forms like *Centrophorus squamulosus*, *C. granulosus*

and *Scyllium canicula*. If, on the other hand, we regard it as that part of the intestine into which the pancreatic and bile ducts enter then it is always present although in certain forms, as in *Heptanchus* and *Hexanchus*, this is simply that part of the intestine containing the first fold of the spiral valve and the only point distinguishing it is the fact that the ducts enter it. Whichever of these definitions we adopt it hardly seems justifiable to say that the duodenum is well defined when, as in *Heptanchus*, the spiral valve invades its whole length. In fig. 131 A in Daniel the letters *p.v.* for the pyloric valve in *Galeus* or *b.e.*, bursa Entiana are misplaced for as they stand they indicate that the bursa is part of the pyloric stomach.

In *Hexanchus corinus* we should say, adopting the first of the viewpoints given above, that a duodenum as a separate morphological entity is not present. So that the next part of the alimentary canal after the pylorus is the valvular intestine.

The part of the intestine occupied by the spiral valve is about 12 inches long and the valve itself contains thirty-six folds. Parker (14) recognises four types of spiral valve in the Elasmobranchs and that in *Hexanchus corinus* is of the type that he designates type C (p. 54) in which "all the turns but the first are deflected backwards, the width of the valve becoming much greater than the semidiameter of the intestine." Such a form is illustrated in the cases of two species of *Raia* but in the present specimen it is still more marked and hence it illustrates type C better than Parker's own examples. The spiral valve is thus of a totally different type from that in *Scyllium* where we find a series of almost cones with their apices directed anteriorly so that the food passes along their outer edge, i.e. the one attached to the intestinal wall, in order to get to the next turn. Instead of this we find a series of almost truncated cones with their apical ends directed posteriorly and so the food passes towards the inner edge of the valve away from the line of insertion. The last four or five turns of the spiral have their inner edges passing back to about the same level so that on looking at the posterior end of the whole valve we see a spirally wound membranous edge of from four to five whorls. The pyloric valve projects into the intestine for about an inch and the beginning of the first fold of the spiral valve is attached to the whole of this.

According to Hawkes (6) the spiral valve in *Chlamydoselachus anguineus* is of somewhat the same type, for that author says "of the 43 coils in my specimen 7 pass forwards, 1 is contorted and 35 are directed backwards." Parker states that in *Notidanus* (presumably *Heptanchus*, *Notorhynchus* or *Heptanchus cinereus*) the valve consists of twenty turns and is intermediate between types B and C and "approaching more nearly the former i.e. with the valves equal in width to the semidiameter of the intestine." Daniel found a valve of 17–18 turns in *Heptanchus maculatus* but of the same type as in *Scyllium* and this appears a noteworthy distinction between it and the other primitive sharks just mentioned and *Hexanchus corinus*.

Beyond the spiral valve the intestine decreases noticeably in size and passes

from the right side of the body cavity to the middle line where the rectal gland joins it. From this point it may be regarded as the rectum which is a fairly narrow tube passing straight back to open into the cloaca and is attached to the mid dorsal line by the posterior moiety of the mesentery.

In Elasmobranchs in general we find that the rectal gland is a finger-shaped structure attached to the junction of intestine and rectum by a narrower portion which forms a kind of stalk. Daniel (vol. I, 127) states that in *Heptanchus maculatus* "the rectal or digitiform gland...is a finger-like structure which is composed of multitudes of gland cells and which empties by a central lumen into the intestine." But in a very good illustration (fig. 117) it is clearly illustrated as an ovoidal structure whose surface is raised into a number of rounded lobules quite unlike the condition in the Squalidae like *Squalus acanthias* or in the Raiidae like *Raia clavata*. In *Hexanchus corinus* we find yet another condition. Here the rectal gland consists of a main mass, in the present specimen about 2 inches square and nearly $\frac{1}{2}$ inch thick, composed of five digitiform and almost but not quite separated lobules, each of which possesses its own lumen. The five lobules run together to form the stalk, also about 2 inches long, into the single duct of which the five lumena open. It is attached to the mid dorsal line of the coelom by the front end of the posterior mesentery. We see then that the rectal gland in this species is of a unique type.

The liver is constituted much as in *Squalus* or *Scyllium* of two main lobes, a right and a left, joined together anteriorly and attached to the pericardio-peritoneal septum by a median, stout, suspensory ligament. From the ventral region of the anterior mass arises a small, ventrally lying, lanceolate lobe in which lies the elongated gall bladder. The main lobes lie lateral to the alimentary canal, pass almost to the posterior end of the coelom, and are crescentic in ventral view and almost triangular in cross-section, being hollowed on their mesial borders to fit round the other viscera. The left lobe is bigger than the right and in the specimen measured 34 inches along its mesial border and $43\frac{1}{2}$ inches along its lateral border against 33 and $41\frac{1}{2}$ inches respectively. The whole organ as in sharks in general was extremely oily.

The ductus choledocus is a well-marked, strong-walled, tube running from the gall bladder in the anterior mesentery dorsal to the coeliac artery to open into the top end of the intestine in the region of the first fold of the spiral valve. The exact relations of the hepatic ducts and of the point of entry of the ductus choledocus was not worked out.

The pancreas is of much the same general form as in *Scyllium canicula*. It consists of an anterior, dorsal lobe lying dorsal to the anterior curve of the pyloric limb of the stomach and passing in front of it. This is relatively larger and more anteriorly situated than in *S. canicula*. The ventral lobe is also a large mass lying ventro-laterally to the space between the pyloric stomach and the valvular intestine. The two are joined by a median, laterally compressed lobe passing dorso-ventrally behind the curve of the pyloric end of the stomach. The omenta in the region of the median and dorsal lobes of the pancreas and

the pyloric region form a curious sac-like pocket ending blindly anteriorly. The right side of the ventral lobe of the pancreas is closely attached to the wall of the intestine in the region of the first fold of the valve by a tough mesentery. The fenestrated omentum that binds together intestine, pyloric and cardiac stomach is inserted into the former by a thick band and also gives off a ventrally running sheet that is attached to the mid dorsal line of this lobe of the pancreas. Thus between this ventrally running sheet, the more dorsally situated portion of the fenestrated omentum, the right side of the dorsal surface of the ventral lobe of the pancreas and the left antero-lateral region of the intestine we find another quite large cul-de-sac with its blind end directed posteriorly. The various lobes of the pancreas have a common duct which apparently arises from near the union of ventral and median lobes, passes into the wall of the intestine and round this a short way before opening internally not far from the first fold of the spiral valve and the aperture of the bile duct.

The spleen in the Elasmobranchs in general lies at the posterior end of the stomach at the junction of cardiac and pyloric limbs and in most cases is a compact body as in *Scyllium canicula* and *Squalus sucklii*. In *Hexanchus corinus* we find a condition more nearly resembling that in *Heptanchus maculatus* as described by Daniel. The spleen is a band-shaped strip of dark coloured tissue broken up into a series of lobes arranged in a moniliform manner and each attached by its own omentum. The largest lobe is at the junction of the cardiac and pyloric limbs of the stomach, a series of smaller lobes lie along the right side of the pyloric stomach to which each is attached by a gastro-splenic omentum. Another lobe lies in the bend at the anterior end of the pyloric limb and a small one by the side of the intestine close to the line of attachment of the ventral lobe of the pancreas. Finally there is quite a large separate lobe about 6 inches long, 2 inches wide and $\frac{3}{4}$ inch thick lying in the anterior mesentery posterior to the coeliac artery. The presence of this large isolated lobe or supplementary spleen appears to be a feature found in several Squalidae, for example, *Centrophorus calceus*, *C. granulosus*, *C. squamosus*, etc.; *vide* Woodland ((17), p. 874).

BLOOD VASCULAR SYSTEM

In this system the difficulties in the matter of nomenclature become much more acute than elsewhere. These arise from the fact that the terminology sometimes employed is adopted from mammalian and chiefly human anatomy and the name, with or without a qualifying adjective, is often applied to vessels that are not homologous. Or, if the vessel is comparable, a name implying a strictly mammalian condition is applied. A glaring example of the latter is at once obvious in the internal mammary artery. How can a comparative anatomist use such a name for a vessel, apparently always the same morphologically, that is found in Fish, Amphibia, Reptiles and Birds? The present is not the place to discuss these vexed questions, although unfortunately they are bound to intrude, and as far as possible a conservative nomenclature is

adopted, although its inadequacy is recognised and in a few instances an alteration suggested.

The pericardial cavity is as usual large and triangular in shape with the apex pointing forward. It is $4\frac{3}{4}$ inches wide and $3\frac{1}{2}$ inches long. Two pericardio-peritoneal canals lead from the pericardial cavity into the general body cavity;

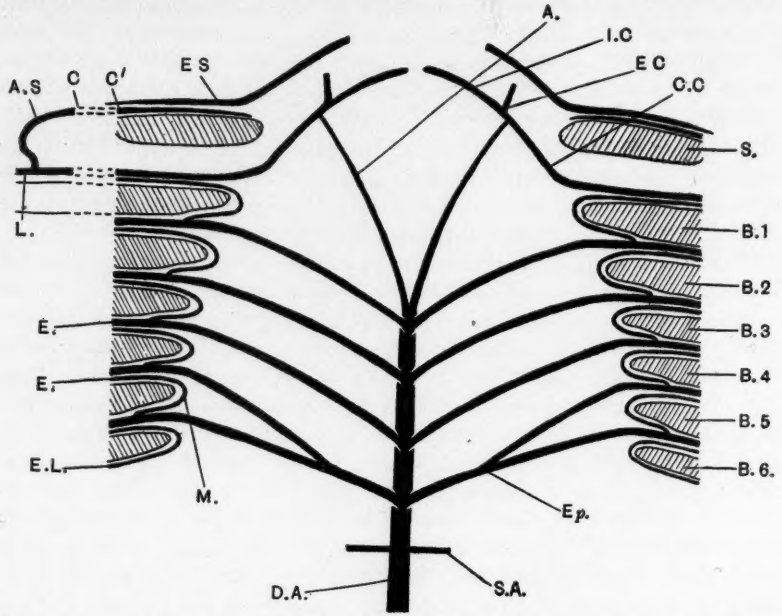


Fig. 2. Diagram of the Efferent Branchial System of *Hexanchus corinus*. *A.* anterior prolongation of aorta; *A.S.* afferent spiracular artery; *B.* 1–6, branchial clefts 1–6; *C–C'*, portion of spiracle, hyomandibular region and associated vessels omitted; *c.c.* common carotid; *D.A.* dorsal aorta; *E.* efferent branchial artery; *E.C.* external carotid artery; *E.L.* efferent branchial artery of the small hemibranch on the posterior wall of the last cleft; *Ep.* epibranchial artery; *E.S.* efferent spiracular artery; *I.C.* internal carotid artery; *L.* lateral angle of Hyoidean cleft; *M.* mesio-dorsal portion of the efferent branchial artery; *S.* internal spiracular cleft; *S.A.* sub-clavian artery.

The large efferent on the posterior wall of the cleft no doubt communicates with the small efferent on the anterior wall of the cleft immediately behind it. But such communications were not dissected out so that, as their number and position are not known, they are not inserted in the diagram.

they are visible as two small, but quite distinct, circular apertures about an inch apart, lying dorsal to the sinus venosus.

The sinus venosus is a thin-walled, elongated, triangular sac, $4\frac{3}{4}$ inches long, its posterior wall is formed the pericardio-peritoneal septum. The hepatic sinuses open through this wall by fairly large, slit-like apertures, not guarded by valves and separated by about $1\frac{3}{4}$ inches. To the left of the middle line its anterior end is attached to the junction of the atrium and ventricle about

$1\frac{1}{2}$ inches from the septum and, on the right of the middle line, to the atrium only and about $\frac{1}{2}$ inch further forwards. The lateral extremities have a diameter of about $\frac{1}{2}$ inch just at the limits of the pericardium where they receive the ductus Cuvieri.

The atrium is a roughly triangular sac which in its empty and fully contracted condition is about $2\frac{1}{2}$ inches wide and $1\frac{1}{2}$ inches long. When contracted it exhibits a series of low, approximately radiating folds and the greater part of it lies anterior to the ventricle. The sinus venosus opens into it near the middle line by a well-marked sinu-atrial aperture guarded by a pair of almost semi-circular sinu-atrial valves disposed dorso-ventrally. When fully expanded the sinus occupies all the anterior end of the pericardial cavity.

The ventricle is a large, very thick-walled, muscular sac, almost quadrangular in shape but asymmetrical. The posterior, bluntly rounded apex is directed backwards and overlies the sinus venosus slightly to the right of the middle line. The more obtuse blunt angle in the base of the ventricle from which the conus arises is still more to the right of the middle line. If a line be drawn from the conus to the apex, practically two-thirds of the ventricle lies to the left of it. In its fully contracted state the ventricle measures $2\frac{1}{2}$ inches across by 2 inches long. The atrium communicates with the ventricle at the front left-hand corner of the latter by a large atrio-ventricular orifice guarded by a similarly named valve composed of a pair of transversely running, strong flaps lying on the dorsal and ventral walls of the ventricle behind the aperture. The plane of these valves therefore is at right angles to that of the sinu-atrial valves.

The conus arteriosus is a tubular structure about 2 inches long arising from the ventricle to the right of the middle line and as it passes forwards it inclines slightly so that it leaves the pericardial cavity in the mesial line. It is narrowest at the point where it leaves the ventricle where it is just less than $\frac{1}{2}$ inch in diameter but further forward it has a diameter of slightly more than $\frac{3}{4}$ inch. Its wall is not much thicker than that of the atrium but is much tougher. Inside it we find a series of deep pocket-like valves arranged in four transverse rows, three rows near the base and one at the apex of the conus. Each transverse row consists of three valves. The proximal row consists of three almost rectangular membranous flaps, broader than long, which lie in the same plane but do not touch. The anterior edge of each valve is curved up into a blunt point in the middle and is tied on to the wall of the conus by two or three tendinous cords near each corner. The side of each valve is thickened into a sort of cord which is continued back beyond the posterior edge for a short distance. The next two rows of valves are similar in structure but narrower so that the most anterior are almost square and are separated by intervals wider than themselves. The function of these valves is not obvious, for in the foremost of the three rows they could not do more than partially close the lumen of the conus.

The most anterior row consists of three much larger valves which are so

wide that their front corners practically touch one another. Each valve gets narrower as it passes backwards and is noticeably longer than wide. The middle is strengthened by a more thickened muscular ridge which projects anteriorly as a blunt point and is continued back from the valve a short distance as a rod-like ridge, enlarges to form a knob and then passes into the general wall of the conus. These three flaps while not tied by cords anteriorly are quite large enough to completely block the lumen of the conus. The form and arrangement of the conus valves are very similar to those in *Heptanchus maculatus*.

The coronary arteries arise from the hypobranchial system although unfortunately the details of the latter were not investigated. At the origin of the ventral aorta the coronary vessel on each side divides into two, a dorsal branch which passes over the dorsal wall of the pericardial sinus as the pericardial artery and a ventral branch, the coronary artery *sensu strico* which runs down the dorso-lateral wall of the conus. The left coronary artery is larger than the right and near the junction of conus and ventricle it gives off a fair-sized dorsal branch that serves the atrium. When it reaches the junction of conus and ventricle each coronary artery divides into a series of dorsal and ventral branches which spread out in a fan-like manner. It may be that the asymmetry of the two arteries was an individual variation in this particular specimen since there is a certain amount of variation in these vessels in other Elasmobranchs, e.g. *Scyllium canicula*, *Squalus acanthias*, *S. sucklii* and *Raia erinacea*. It seems more probable however that it is normal since, as described above, the atrium is attached to the left side of the ventricle and this chamber is itself asymmetrical, the left side being larger than the right.

The coronary veins accompany the arteries and apparently enter the sinus venosus by two apertures near the sinu-atrial valves.

The ventral aorta is a fairly large, soft-walled tube of white colour passing forwards from the conus arteriosus and commencing immediately outside the pericardial cavity. It is about 5 inches long and at its origin about $\frac{3}{4}$ inch in diameter. At its front end, behind the mandibular symphysis and ventral to the basihyal cartilage, it divides into two innominate arteries which pass straight laterally for about 1 inch. Here each divides into two approximately equisized vessels, the anterior branch, the hyoidean afferent, supplies the hyoidean hemibranch, and the posterior branch, the first branchial afferent, supplies the first holobranch. The second branchial afferent arises from the ventral aorta $1\frac{3}{4}$ inches behind the first; the third, $1\frac{1}{4}$ inches behind this; the fourth, 1 inch further back; and the fifth, close behind the fourth. Each afferent passes right round the gill bar gradually diminishing in size and finally disappearing at the dorsal end of the gill.

The whole afferent system is on the same general plan as in other Elasmobranchs, the striking feature being the presence of six afferent arteries.

The blood is carried from the gills to the dorsal aorta by a collector system that presents several peculiarities. It may be recalled that in *Scyllium canicula*

there is a fairly well-marked efferent loop around the first four gill pouches and the four epibranchial arteries arise from the dorsal points of these loops. The epibranchial in this form, then, practically comes from the edge of the cleft where it is formed by the union of the efferent from the anterior and that from the posterior hemibranch and these two arteries are about equal in size. In *Hexanchus* as in *Heptanchus* (*vide* Daniel, p. 166) the epibranchial arteries arise from the gill bars, except the hyoidean bar, between the pouches as the continuation of large efferent branchial vessels. This difference between the Notidanids and *Scyllium* is more apparent than real for we find in *Hexanchus* that each efferent branchial artery, about $\frac{3}{4}$ inch from the dorsal end of the gill pouches between which it runs, that is, well lateral to the dorsal limit of the gill filaments, gives off a small vessel on its anterior side. This tiny artery passes mesially along the base of the posterior hemibranch, around the dorsal end of the gill cleft and into the base of the anterior hemibranch of the same pouch. It thus represents the mesio-dorsal portion of the loop in *Scyllium*. A similar small artery is present also on the ventral end of each cleft constituting the mesio-ventral portion of the loop in *Scyllium* and related to the adjacent hemibranchs just in the same manner as its dorsal equivalent. Branches are given off from these ventral vessels presumably to form a hypobranchial system.

In *Heptanchus* these two little vessels are in continuity along the base of the anterior hemibranch, thus constituting a complete efferent or collector loop. The large efferent vessel is closer to the base of the posterior hemibranch of the pouch in front and is joined to the small efferent by numerous anastomoses so that no doubt it is responsible for the major part of the drainage of the complete holobranch. The condition in *Hexanchus corinus* is probably much the same although the smaller vessel is quite tiny and circumstances did not permit of its being traced, the length of the hemibranch. It was only followed for an inch or so in several of the gill bars.

As we have seen in *Hexanchus*, unlike *Heptanchus* there is a small hemibranch on the posterior wall of the last gill cleft and this is taken care of by a small twig passing around the dorsal end of the pouch as in the other pouches, but it is the sole means of draining this hemibranch since no large artery as in the more anterior clefts is present. Small though it is this vessel may be of some significance since in higher animals, when lungs develop, they receive their supply from a vessel arising from a dorso-lateral point posterior to the last gill slit and entering the last epibranchial. In other words, in just such a position as the vessel we have just described.

The first epibranchial artery can be considered as arising just where the pharyngeo-branchial and epibranchial cartilages join at the dorso-mesial end of the gill cleft. The first of them passes mesially along the postero-dorsal border of the first pharyngeo-branchial while the remainder, for the main part of their course, lie dorsal to their corresponding skeletal bars. The last two epibranchial arteries join about an inch and a half before reaching the aorta. In *Heptanchus maculatus* they also join but much closer to the middle line.

The two corresponding epibranchial vessels from each side unite to form a common trunk just before entering the aorta.

The anterior wall of the first, i.e. the hyoidean, gill pouch possesses an efferent branchial artery (sometimes called an efferent collector) similar to the others but slightly larger and, unlike them, not united to the aorta by an epibranchial artery. From its antero-dorsal corner arises the common carotid (hyoidean efferent) artery. The common carotid passes in a curve mesially and forwards along the base of the cranium and some distance along it is joined by an anterior prolongation of the dorsal aorta which takes origin immediately at the point where the common trunk of the first epibranchials enters this vessel. In *Squalus sucklii* the anterior epibranchials actually enter well in front of the bifurcation of the aorta and in *Heptanchus maculatus* immediately anterior to this point. Thus in this respect *S. sucklii* can be considered as more primitive since it retains relatively more of the original paired dorsal aortae.

After receiving the branch from the aorta the common carotid divides into external and internal branches. The external carotid runs forwards and slightly outwards to perforate the postero-lateral wall of the orbit. Its course and distribution beyond this point were not followed. The internal carotid artery continues on in the line of the common carotid until about $\frac{3}{16}$ inch from the mesial line where it enters the basal cartilage of the cranium. Thus the two internal carotids enter the cartilage separately but at an angle to one another so that they unite to form a single trunk just as they enter the cranial cavity.

At the lateral angle of the hyoidean gill pouch the anterior efferent branchial gives off a marked branch, the afferent spiracular artery, which runs close to and around the hyomandibular cartilage to its dorsal side and then forwards and inwards to the spiracular hemibranch. This is the pseudobranchial artery of Daniel (p. 167) but the name does not appear well chosen for in *Heptanchus maculatus* as in *Hexanchus corinus* there is no pseudobranch but simply a small hemibranch and presumably this was the ancestral condition. The older names for this vessel are hyoid artery, anterior carotid or ventral carotid, all of which are open to objection. The name afferent spiracular artery has been suggested because it does not imply any homologies with vessels in the higher animals and does suggest the functional relational relationship of the vessel, namely that it conveys blood to the spiracular region. It also does not matter whether a hemibranch or a pseudobranch is present upon the anterior wall of the spiracle. In the main the afferent spiracular artery breaks into numerous branches supplying the spiracular hemibranch although some twigs also go to the surrounding tissues. The hyoidean efferent continues on around the gill pouch and at its ventral extremity breaks into branches, one of which passes forwards towards the mandible. The others were not followed in details.

The blood is collected up from the spiracular hemibranch by an efferent spiracular artery (this name seems preferable to ramus anastomoticus) which is ventral to the afferent vessel and runs forwards and inwards, perforating the posterior floor of the orbit. Presumably it gives off branches and then

enters the lateral cranial wall as in *Heptanchus maculatus* and other Elasmobranchs like *Scyllium*, *Squalus* and *Raia* but actually its course was not followed.

The dorsal aorta passes backwards from the point of entry of the last epibranchials in the base of the mesentery, then along the dorsal wall of the coelom until it reaches the place where the caudal mesonephroi join in the middle line. It passes dorsal to this and where the mesonephroi separate it reappears again but only to pass out of the coelom into the haemal canal of the caudal vertebrae. As usual, the dorsal aorta gives off paired parietal arteries throughout its length and in the anterior half of its course these pass across the post-cardinal sinuses. The subclavian arteries, apparently modified parietals, arise behind the point of entry of the last pair of epibranchials as in *Heptanchus maculatus* and not anterior to them as in *Scyllium canicula*. The next large, paired arteries are the iliacs which originate from the aorta shortly before it leaves the coelom.

Here and there along the length of the cranial mesonephroi branches from the parietals are given off to those bodies but in the region of the caudal mesonephroi each parietal gives a well-marked renal branch to the kidney.

A pair of arteries, either modified parietals or marked branches therefrom, arise a short distance behind the subclavians and run to the anterior ends of the oviducts so constituting the oviducal arteries.

The arterial supply to the alimentary canal varies very considerably throughout the Vertebrata. In general, in long bodied forms, i.e. those with a relatively long coelom such as Urodela, Coecilians, some lizards and the snakes, a number of branches from the aorta supply the gut. In short bodied forms such as frogs, toads and most mammals, this number is reduced. The dangers of trying to fit the conditions in lower forms in to those found in a highly specialised group like the Mammalia have already been noted and we fear that Daniel has tried to do this when he states (p. 170): "The arteries given off from the dorsal aorta to the digestive tract consist of three large trunks, the coeliac axis, the anterior mesenteric and posterior mesenteric arteries." Two pages further on he himself admits that "the superior mesenteric (*s.m.*, fig. 153) as such is usually absent in *Heptanchus maculatus* and when present it is never more than a short stem...." If any evidence is to be derived from the embryo it would appear that on the whole the primitive condition in the Elasmobranch was a relatively long coelom such as is most nearly retained in forms like *Heptanchus*, *Hexanchus*, *Squalus* and *Scyllium*. In these forms we find normally four large vessels serving the gut, generally termed the coeliac, the anterior mesenteric, the lieno-gastric and the posterior mesenteric. Indeed as Daniel points out (p. 190): "This condition is characteristic of many types of which it should be said that no true superior mesenteric artery exists." This indeed appears to be the more primitive, and is certainly the more common, condition and when anterior mesenteric and lieno-gastric fuse to form one trunk in Elasmobranchs it should be regarded as an anomalous condition as in *Squalus acanthias* and *S. sucklii* where it occurs rarely or as an indication

of a relatively shortened coelom which is obviously the case in *Heterodontus francisci*. The adjectives anterior and posterior also seem more suitable than superior and inferior.

The arrangement of the four arteries in *Hexanchus corinus* is much the same as in *Squalus*. The coeliac artery is a large vessel arising well forward under the oesophagus and passing to the right of the proximal lobe of the stomach. It gives off a short gastro-hepatic branch which soon divides into a hepatic artery, going to the liver and bile duct, and a gastric artery. The latter is distributed to the cardiac end of the stomach and its branches run alongside those of the anterior gastric vein which is described more fully below. The main part of the coeliac goes on as the anterior intestinal, giving branches to the pancreas, the pyloric enlargement, the front end of the pyloric end of the stomach and the lobes of the spleen adjacent thereto. It then continues on down the latero-ventral wall of the intestine and it and its branches accompany those of the posterior intestinal vein (*vide infra*). Doubtless it gives off an intra-intestinal artery but this was not traced. The anterior mesenteric artery arises some distance further back and runs to the dorso-lateral wall of the intestine and ramifies with the posterior intestinal vein. The lieno-gastric artery arises immediately behind this and crossing it passes to the dorsal posterior wall of the cardiac end of the stomach, the hinder part of the pyloric loop and the lobes of the spleen in this region, partly accompanying the ramifications of the median gastric vein. The posterior mesenteric artery in this specimen is a single vessel originating from the dorsal aorta considerably further back than the foregoing artery and passing to the anterior corner of the rectal gland which it supplies. The origins and distribution of these splanchnic arteries are very similar to those in *Heptanchus maculatus*.

In order to preserve the brain and anterior cranial nerves intact no dissection of the anterior veins was made.

The alimentary canal is drained by a hepatic portal system as in Vertebrates in general.

The posterior intestinal vein arises on the front end of the rectal gland, passes down it and its stalk to the wall of the intestine, along the latero-dorsal wall of which it runs practically to the anterior end. During its course it receives about fourteen well-marked branches from the lines of insertions of the folds of the spiral valve and as some of these have two or even three factors practically all the thirty-six insertions are taken care of. At the top of the intestine near the level of the point of entrance of the bile duct it leaves the intestinal wall and runs forwards parallel with the duct to a point about 2 inches below the point of entry of the anterior gastric vein where it unites with the anterior intestinal. In not leaving the intestinal wall until the front end this vessel differs from the similar one in *Heptanchus maculatus*, *Squalus* and *Scyllium* and indeed a number of Elasmobranchs. It differs from the vein in *Scyllium* (13) but resembles that in *H. maculatus* in continuing forward well in front of the pyloric region.

The anterior intestinal vein (ventral intestinal) commences about 4 inches in front of the level of insertion of the stalk of the rectal gland and runs up the latero-ventral wall of the intestine, receiving numerous factors from the lines of insertion of the folds of the spiral valve. It leaves the intestinal wall to pass dorsally to the ventral lobe of the pancreas, being partly embedded for a short distance, where it receives pancreatic factors, in the dorso-mesial border of that structure. Thence it runs parallel with the posterior intestinal vein to join it as indicated above. The anterior intestinal vein receives factors from the front end of the intestine and presumably one of these is the intra-intestinal vein although this was not dissected. It also receives a branch from the pyloric end of the stomach and the lobes of the spleen adjacent thereto. The constitution and disposition of this anterior intestinal trunk is very similar to that in *H. maculatus* and noticeably different from that in *Scyllium* (13).

The median gastric (gastro-splenic) vein takes origin on the dorsal side of the junction between the cardiac and pyloric regions of the stomach in a union of vessels from the posterior lobes of the spleen and the postero-dorsal side of the cardiac stomach. It runs along the dorso-lateral side of the cardiac part of the stomach and then leaves it to run freely in the mesentery. Here it receives a branch from other lobes of the spleen and the proximal portion of the pyloric stomach and finally enters the anterior intestinal vein just in front of the curved distal end of the pyloric portion of the stomach. This vessel also more nearly resembles that in *H. maculatus* than that in *Scyllium*.

The anterior gastric vein is a short trunk leaving the dextro-lateral wall of the stomach just below the end of the oesophagus and running freely and laterally to enter the common trunk, i.e. the hepatic portal vein, formed by the union of anterior and posterior intestinal veins 2 inches in front of their junction. It is formed by the union of three main factors. The first of these is constituted by the confluence of numerous deep branches from each surface (dorsal and ventral) of the oesophagus and so may be termed the oesophageal. The second drains the anterior end of the cardiac portion of the stomach on each side over which it spreads out. The third arises a short way up the pyloric limb of the stomach and then passes forwards up the dextro-lateral wall of that organ along the line of insertion of the fenestrated omentum. It receives five or six well-marked factors from both the dorsal and ventral aspects of the stomach. The general disposition of the anterior gastric vein while fundamentally the same as in *Heptanchus maculatus* differs in that the three main factors are not long nor so free from the wall of the stomach and recalls the condition in *Squalus acanthias*.

After receiving the anterior gastric vein the hepatic portal trunk runs up in the main mesentery parallel with the bile duct, receiving as it does so one large and some smaller factors from the anterior isolated lobe of the spleen and just before reaching the liver it divides into two large branches, one going to each main lobe.

It will be noticed then that, on the whole, the constitution of the entire

hepatic portal system approximates most closely to that in *Heptanchus maculatus*.

The blood is taken from the liver to the sinus venosus by two large hepatic sinuses which do not run together as in *Scyllium*. These perforate the pericardio-peritoneal septum by two separate slit-like apertures about $1\frac{3}{4}$ inches apart.

The renal portal veins pass up the dorso-lateral margins of the caudal mesonephroi and are completely separated in the middle line. They diminish in size as they pass forwards and, when opened up, the side of the kidney abutting their ventro-mesial wall is seen to be perforated with numerous circular pores which are the opening of the venae renales advehentes.

The posterior cardinal sinuses commence as a single median interrenal vessel in the region where the mesonephroi touch in the middle line. It was not clear whether this vessel represented the posterior part of the right posterior cardinal as in *H. maculatus* and *Mustelus antarcticus* or whether it was the fused ends of the two posterior cardinals as in *Scyllium* and *Raia*. About 8 inches up the two post-cardinals are separated in the middle line and remain so for the rest of their course, not partially fusing again as in *Scyllium*. For the greater part of their length the post-cardinals are large flattened vessels, running under the peritoneum parallel with and dorsal to the dorsal aorta, with a diameter of about $\frac{1}{2}$ inch, but at the anterior end they diverge and expand to form wide sinuses relatively larger than in *H. maculatus*. The lateral walls of the interrenal region and the hinder end of the separate post-cardinals are perforated with a series of circular apertures which are the openings of the venae renales revehentes. During their course along the dorsal body wall their dorsal sides are perforated by the apertures of the parietal veins which lie somewhat laterally and slightly in front of the corresponding parietal arteries.

The relationships of the anterior and posterior cardinal sinuses to one another and to the ductus Cuvieri are quite different from those described by Daniel for *H. maculatus* and resemble much more closely those in *Scyllium canicula* (13). The ductus Cuvieri appears as a soft-walled tube projecting about $2\frac{1}{2}$ inches along the front wall of the posterior cardinal sinus. The anterior cardinal sinus opens into the posterior by a transverse slit-like aperture guarded by membranous flaps and situated about 2 inches lateral to the opening of the ductus.

UROGENITAL SYSTEM

In spite of the size of the specimen it was, as noted previously, a young female and the reproductive organs had not reached a very advanced stage of development.

The ovaries are paired masses of tissue lying far forward in the coelom and about 4 inches long by 1 inch at their widest part and $\frac{1}{4}$ inch thick. The

posterior part consisted of a small lobe-like mass of smooth tissue perhaps to be regarded as the remains of an epigonial organ. The much larger anterior part was slightly lobed and the front lobes were distinctly though only faintly granular, the individual granules no doubt representing ova in an early stage of formation. Each ovary was attached slightly to the side of the mid-dorsal wall of the coelom by a stout mesovarium which commenced well up under the oesophagus in front of the ovary and extended back behind it for some distance. In the mesovarium quite close to, but just mesial of the ovary, is a narrow band of tissue, harder than the ovary, which appears as a sort of raised ridge. Unfortunately while its presence was noted its significance was overlooked while dissecting the animal and so none of it was preserved for sectioning. No doubt it is the tissue described by Semper(16) in *Hexanchus griseus* and stated by him to be a rudimentary testis. A similar band of tissue is present in *Heptanchus maculatus* according to Daniel (vol. I, 303). If the identification of this tissue made by Semper is correct it is interesting to find a condition of partial hermaphroditism in these three primitive Elasmobranchs.

The two oviducts open by a common oviducal aperture lying in the median line on the ventral wall of the oesophagus up under the central portion of the liver. They pass laterally around the oesophagus to lie on the dorsal wall of the coelom and while small are nevertheless quite distinct. They are to be traced backwards and end blindly under the skin of the cloaca but while close together do not seem to have (in the young specimen at any rate) a common terminal chamber as in many Elasmobranchs. Thus there are apparently two hymena right side by side instead of one. Just posterior to the point where the front end of the oviduct passes from the lateral wall of the oesophagus on to the dorsal coelomic wall, the duct enlarges slightly. This swelling is more vascular than the rest of the oviduct and represents the rudimentary oviducal gland. The posterior end of the oviduct, where it passes along the caudal mesonephros, is somewhat larger than more anteriorly.

On the whole the urogenital system is very similar to that in *Heptanchus maculatus* as described by Daniel (vol. I, 303).

Unfortunately the urinary system had been partly dissected away before I was able to examine it so that the notes on this part are not so full as I should like.

The cranial portions of the mesonephroi while neither so wide nor so deep as the hinder parts are nevertheless quite distinct. The caudal mesonephroi are well developed, compact organs and about 13 inches long. Not quite half way back they come into close apposition ventrally so that they apparently form one body posteriorly, thus covering over the last part of the interrenal portion of the post-cardinal sinuses. In front of the cloaca they again separate and pass deeply into the dorsal body wall for about $1\frac{1}{2}$ inches.

The ureters apparently commence at the anterior end of the cranial mesonephroi as tiny tubes but increase noticeably in size at the beginning of the caudal mesonephroi. As they pass back they receive a fairly regular series of

factors and then unite in the middle line to form a common urinary sinus which opens into the cloaca on the single urinary papilla.

No structures corresponding with the cloacal pits of *Scyllium canicula* are present but the cloacal papillae are well marked. Each is perforated by a distinct abdominal pore which gives direct access to the coelom.

NOTE ON THE STRUCTURE OF THE LYMPHOID ORGAN (ORGAN OF LEYDIG) AND SPLEEN OF *HEXANCHUS CORINUS*

By LLOYD L. BOLTON

THE peculiar lymphoid organ, or organ of Leydig, found only in the wall of the oesophagus of Elasmobranchs was first demonstrated by Cuvier and first described in some detail by Leydig (12) in 1852. Since then its structure in a number of species has been described, particularly by Drzewina (3, 4, 5) and Kulchitzkii (10). Of its exact analogies and functions little seems to be known. Drzewina (5) describes its early development, and also notes that it becomes much more active after splenectomy, suggesting that it probably is an important centre of origin of leucocytes. For a very complete bibliography and review of the previous literature, the reader is referred to Drzewina (4). The structure of the organ in the skate (*Raia clavata*) is described by Kulchitzkii (10), who gives numerous staining reactions of the different types of infiltrating cells present.

Drzewina describes five types of cells infiltrating the loose connective tissue reticulum, viz:

(1) Granular cells with small acidophilic granules and an eccentric loosely constructed nucleus, which may be lobulated.

(2) Polymorphonuclears, similar to the granular cells, but with a double or many-lobuled nucleus.

(3) Lymphocytes with a large nucleus and little cytoplasm. It is suggested that these may be converted into cells of the granular type.

(4) Mononuclears with a central nucleus and a large quantity of homogeneous cytoplasm.

(5) Polymorphonuclears with homogeneous cytoplasm. These are rare. Kulchitzkii describes in the skate:

(*a*) Leucocytes with coarse eosinophilic granules and a peripheral nucleus which may be flattened.

(*b*) Leucocytes with fine eosinophilic granules and an ovoid or flattened nucleus.

(*c*) Lymphocytes with little cytoplasm, and also some of a larger type with a very loose nuclear structure.

(*d*) Neutrophiles—large cells with a polymorphic nucleus.

In the two types of granular leucocytes and lymphocytes, he notes that

the nuclei may be of the normal more or less uniform structure, or they may appear to have within them a series of canals. Drzewina also notes that the chromatin structure may appear loose and vesiculated.

In *Hexanchus corinus* the lymphoid organ was a large mass which would weigh about three or four pounds. The tissue was whitish in colour, and so extremely soft that it could, with very little effort, be pulled apart in coarse stringy masses.

Some small bits of this tissue and bits of the mucosa and muscularis of the oesophagus with the adjacent lymphoid tissue still attached were fixed in Helly's fluid, sectioned in paraffin, and stained in Ehrlich's haematoxylin. The counterstains used were eosin, orange G, and van Giesen's mixture. Other more specialised methods have not been employed, but I trust that a few observations made on these preparations may be of interest.

The general structure of the organ is much like that described for other species, viz., a very loose connective tissue reticulum densely infiltrated with lymphoid cells. Its boundaries are clearly defined in the sections, but there is nothing in the nature of a surrounding capsule. It is highly probable that its limits change with variations in the state of activity of the organ. Infiltrating the reticulum are cells of the following types:

(1) Leucocytes with coarsely granular cytoplasm. The nucleus is large, round or ovoid, and eccentric or peripheral in position. The cytoplasm stains strongly with eosin, orange G and picric acid.

(2) Leucocytes with finely granular cytoplasm. The nucleus is usually slightly larger than that of the coarsely granular cells and shows less uniformity in shape, being commonly flattened or saucer-shaped. It is also usually eccentric or peripheral in position. The cytoplasm stains less brightly than that of the coarsely granular cells.

(3) Lymphocytes with a large round or ovoid nucleus and little cytoplasm. In some the cytoplasm may be increased and show, in parts, fine eosinophilic granules, suggesting that they may be in the process of transformation into granular leucocytes, as suggested by Drzewina(4). Larger lymphocytes are also seen with a looser structure of their chromatin material, and having a greater amount of cytoplasm than the more common small type.

(4) Mononuclears with a round centrally located nucleus surrounded by a considerable amount of non-granular cytoplasm which appears quite homogeneous and stains very faintly bluish in haematoxylineosin preparations, and faintly reddish brown in van Giesen's mixture. The nucleus, like that of the finely granular leucocytes, when stained with van Giesen's mixture only, shows a bright reddish brown colour under high magnification. These cells are very few in number.

No cells resembling the polymorphonuclear leucocytes with finely granular cytoplasm as, described by Drzewina and Kulchitzkii, nor the polymorphonuclears with homogeneous cytoplasm, as described by Drzewina, were found. Many of the granular leucocytes have an irregularly shaped or even bilobed

nucleus, but the variation in form does not seem to be sufficiently marked to consider them as a separate type of cell. It is quite possible, however, that special staining methods might show a greater differentiation within the cell.

In the nuclei of both leucocytes and lymphocytes the loose and the more compact structure of the chromatin material is as noted by Drzewina and Kulchitzkii.

The erythrocytes of the blood are almost entirely confined to the fine thin-walled capillaries ramifying throughout the organ. Their nuclei are round and centrally placed, and stain darkly. The cytoplasm appears quite clear and homogeneous, as a rule.

In the spleen, the same elements occur. The small form of lymphocyte is the cell present in greatest numbers. There are a few of the larger type of leucocyte. The mononuclears with the clear cytoplasm are extremely rare. Of the eosinophiles, those of the finely granular type are the more numerous. The distribution of the granules in the cytoplasm of the finely granular type of leucocyte of the spleen is commonly much less uniform than that of similar cells in the lymphoid organ. Also, in the spleen both types of granular leucocytes show indications of the more active amoeboid movement than they do in the lymphoid organ, for in the spleen they are not so uniformly rounded in shape, but many are found to be distorted in passing between neighbouring cells. Few erythrocytes are found outside the fine capillary channels.

A smaller dark red body was found in the mesentery some 10 or 12 cm. from the spleen. Sections of this show its structure to be almost identical with that of the spleen, and it no doubt was an accessory spleen, an abnormality frequently encountered throughout the vertebrate class.

EXPLANATION OF PLATE

Fig. 1. Photograph of the specimen from the side just after landing. The white object near the lateral line is a small ruler just over 6 inches long.

Fig. 2. Photograph of a dissection of the afferent branchial system. Black paper has been inserted under the vessels to make them distinct and the ruler placed above to give an idea of the approximate size. The approximately rhomboidal and asymmetrical form of the ventricle is clearly shown, likewise the position and nature of the gill rakers on the inside of the last gill bar.

REFERENCES

(1) Daniel, J. F. (1922). *The Elasmobranch Fishes.* University of California Press, Berkeley.

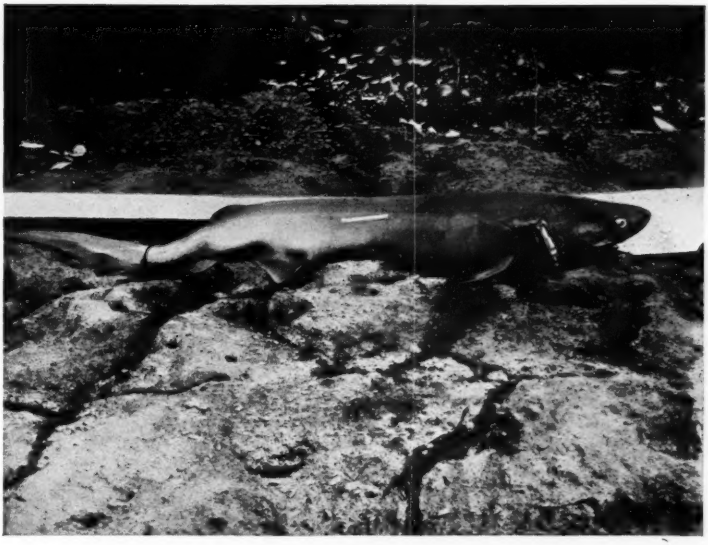
(2) Dean, B. (1895). *Fishes, living and fossil.* Macmillan & Co., New York.

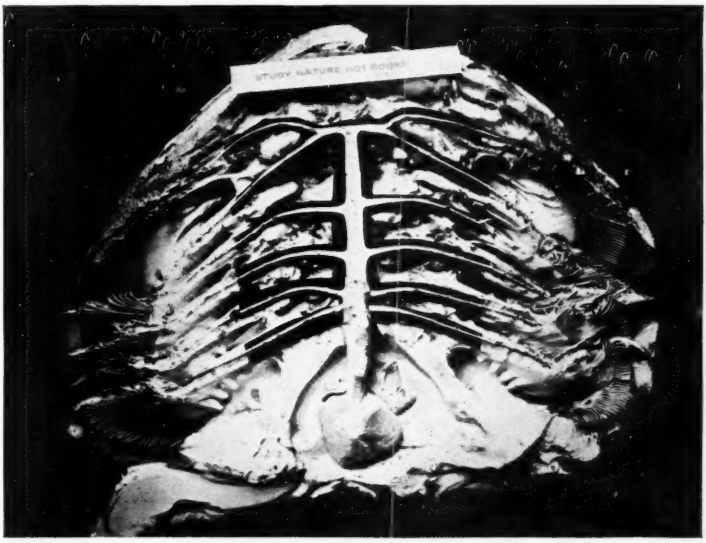
(3) Drzewina, A. (1904). "Sur l'organe lymphoide de l'œsophagus des Sélaciens (Note préliminaire)." *Compt. Rend. Mém. Soc. Biol.* t. LVI, Paris.

(4) —— (1905). "Contribution à l'étude du tissue lymphoide des Ichthyopsides." *Arch. Zool. Expér. Gén.* sér. 4, t. III.

(5) —— (1910). "Sur l'organe lymphoide et la muqueuse de l'œsophage de la torpille (*Torpedo marmorata*, Risso)." *Arch. Anat. Micr.*, Paris, t. XII.

(6) Hawkes, O. A. M. (1907). "On the Abdominal Viscera and a Vestigial Seventh Branchial arch in *Chlamydoselachus.*" *Proc. Zool. Soc. London.*




STUDY NATURE NOT BOOKS

UNIV. OF MICH.

(7) Imms, A. D. (1905). "On the Oral and Pharyngeal Denticles of Elasmobranch Fishes." *Proc. Zool. Soc. London.*

(8) Jordan, D. S. and Evermann, B. W. (1896). "The Fishes of North and Middle America." *Bull. U.S. Nat. Mus.* No. 47, 4 vols.

(9) Jordan, D. S. and Gilbert, C. H. (1880). "Description of a New Species of Notidanid Shark (*Hexanchus corinus*), from the Pacific Coast of the United States." *Proc. U.S. Nat. Mus.* vol. III.

(10) Kulchitzkii, N. (1911). "Ueber das adenoide Organ in der Speiseröhr der Selachier." *Arch. mikr. Anat.* Bd. LXXVIII, Abt. 1.

(11)* —— (1912). *Ueber das adenoide Organ in der Speiseröhr der Selachier.* Charikov.

(12) Leydig, F. (1852). *Beiträge zur mikroskopischen Anatomie und Entwickelungsgeschichte der Rochen und Haie.* Leipzig.

(13) O'Donoghue, C. H. (1907). "Notes on the Circulatory System of Elasmobranchs. I, The Venous System of the Dogfish (*Scyllium canicula*)." *Proc. Zool. Soc. London.*

(14) Parker, T. J. (1880)* "On the Intestinal Spiral Valve in the genus Raia." *Trans. Zool. Soc. London*, vol. II.

(15) Rafinesque, S. (1810). *Caratteri di alcuni nuovi generi e nuove specie di animali principalmente di pesci e piante della Sicilia.* Palermo.

(16) Semper, C. (1875). "Das Urogenitalsystem der Plagiostomen und seine Bedeutung für das der übrigen Wirbeltiere." *Arbeit. Zool.-zoot. Instit. Würzburg*, Bd. II.

(17) Woodland, W. (1910). "On the Anatomy of *Centrophorus calceus* Günther (*crepidalbus* Bocage and Capello)." *Proc. Zool. Soc. London.*

* We have not been able to consult this publication.

ANOMALIES OF THE MYLOHYOID MUSCLE

By P. MALPAS

Demonstrator of Anatomy in the University of Liverpool

The following variations of the mylohyoid muscle were seen recently in the Department of Anatomy in the University of Liverpool.

They possess interest from two standpoints, in their effect on the anatomical relations of the floor of the mouth, and also in their bearing on the morphology of the mylohyoid muscle. In an article on the genial tubercles of the human mandible Professor Arthur Thomson (1) has described a deficiency of the mandibular origin of the mylohyoid muscle in a chimpanzee, and mentions the need for further enquiry into this question.

In four elderly male subjects the mylohyoid muscle of one side was divided into two portions, anterior and posterior, by a gap extending inwards and backwards from a point on the mandible opposite the canine alveolus, to a point in the median raphe, $\frac{3}{4}$ inch in front of the hyoid bone. In three of these instances the hiatus was well marked, and possessed tendinous margins. In the fourth case it did not extend completely to the mandible and had no definitely tendinous edges. In all cases both segments of the muscle were supplied by the mylohyoid branch of the Vth cranial nerve.

In three of the cases the sublingual gland protruded through the gap in the muscle, thus coming to lie one half above, and the other half below the muscle, on the same plane as the superficial part of the submaxillary gland. In the fourth case a small portion only of the gland protruded thus.

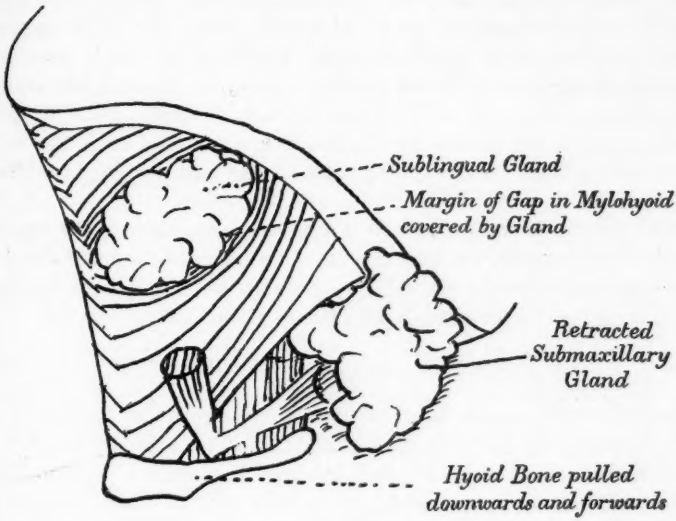
In three of these cases the submental branch of the facial artery supplied a large branch to the protruding sublingual gland, reaching it by passing through the gap in the muscle, and replacing its normal supply from the lingual artery. In the fourth case a similar artery from the facial reached the gland by piercing the muscle behind the gap.

Careful examination of this region in eight further subjects showed that in four instances the sublingual gland received its blood supply by a branch of the submental artery similar to that described above. The artery pierced the mylohyoid muscle, accompanied by numerous lymphatic vessels, at a point corresponding to the centre of the gap seen in the previous specimens.

Dissection of normal specimens of this muscle from the floor of the mouth shows that in contrast to the smooth appearance of its inferior surface, its upper surface is fasciculated, with small processes of the sublingual gland lodged between the fasciculi.

The passage of lymphatic vessels through the muscle, and its intimate connection with the sublingual gland, explain the importance of the mylohyoid muscle in the surgery of carcinoma of the floor of the mouth, and of ranulae.

A further anomaly seen in one specimen was a division of the muscle into two planes. The superficial plane was a thin sheet of muscle arising from the mylohyoid ridge opposite the bicuspid teeth, and passing inwards to end in a thin aponeurosis on the median raphe above the hyoid bone. This sheet was quite independent of the digastric muscle. It was supplied by the mylohyoid branch of the Vth cranial nerve, and no structure passed between it and the deeper layer, which corresponded exactly to a normal mylohyoid muscle.


Sublingual Gland
Margin of Gap in Mylohyoid covered by Gland
Retracted Submaxillary Gland
Hyoid Bone pulled downwards and forwards

The extent of the hyoid attachment of the muscle in this series varied from $\frac{1}{4}$ inch to $\frac{3}{4}$ inch. In two cases the anterior belly of the digastric muscle blended with its inferior surface.

The literature of the mylohyoid muscle is small in amount. Macalister (2) recorded its absence and replacement by the anterior belly of the digastric. It may receive slips from the neighbouring muscles, e.g. the stylohyoid.

Bryce (3) states that division of the muscle into two parts is common. Le Double (4) quotes four cases similar to those described in the first part of this note, of division into anterior and posterior parts. In one of these cases Wharton's duct, and in another the stylohyoid muscle passed through the interval. He does not record any structure passing through the gap in the other two instances. Thomson (1) describes the anomalous mylohyoid muscle

he observed in a chimpanzee as forming a sling below the submaxillary gland between the symphysis and back of the mandible.

In practically all animals the mylohyoid muscle resembles that of man (Young (5), Humphrey (6), Testut (7)). This constancy of structure must be linked with its constancy of function in mastication and deglutition. A division of the muscle into anterior and posterior portions is constant, however, in birds, some reptiles, and the Indian elephant (Cuvier (8)).

It would appear then from the frequency of such a division that the muscle is composed of two morphological units, an anterior forming the diaphragm of the mouth, a posterior being an elevator of the hyoid bone.

If this view be taken, the anterior segment may correspond with the interhyoideus ventralis, and the posterior with that muscle mass, regarded as representing a levator hyoidei, which gives rise to the stylohyoid muscle and the posterior belly of the digastric (Edgeworth (9)). This double origin would explain its fusion with the anterior belly of the digastric and stylohyoid muscles respectively. In such a case its nerve supply must be acquired secondarily, and the factor determining its separation from the adjacent muscle masses must be the development of the salivary glands in the floor of the mouth.

If, on the other hand, the muscle is regarded as arising from the mandibular musculature, its separation from the main mass must be effected similarly by the development of these glands. Bryce states that the muscle may be split into strata by processes of the submaxillary gland.

SUMMARY

The mylohyoid muscle is often divided into two units, anterior and posterior, separated by the sublingual gland, and occasionally by the stylohyoid muscle or Wharton's duct. There is evidence that such a division indicates a compound origin of the muscle, and in that case its nerve supply is not a sure indication of its primitive origin. The perforating sublingual branch of the facial artery may indicate the line of fusion of these units.

The development and form of the muscle are determined by the growth of the submaxillary and sublingual salivary glands.

Its intimate relation to these glands is of clinical importance. Variations in the extent of its hyoid attachment, its fusion with adjacent muscles and its division into layers are described.

My thanks are due to Professor W. H. Wood for much help in the preparation of this note.

REFERENCES

(1) Thomson, A. (1915). *Journ. Anat. and Phys.* vol. L, 45.
(2) Macalister (1875). *Proc. Royal Soc. Ireland*, vol. XXV, 34.
(3) Bryce. Quain's *Anatomy*, 11th ed. Pt. XI, vol. IV, 74.
(4) Le Double (1895). *Variations des Muscles de l'homme*, vol. I, 196.
(5) Young (1882). *Journ. Anat. and Phys.* vol. XVI, 220.
(6) Humphrey (1868). *Journ. Anat. and Phys.* vol. II, 320.
(7) Testut (1896). *Anatomie Humaine*, 3rd ed. vol. I, 632.
(8) Cuvier. Cited by Testut (*loc. cit.*).
(9) Edgeworth (1922). *Journ. Anat. and Phys.* vol. LVII, 328.

ARREST OF DEVELOPMENT OF AN EMBRYO

A CASE OF ACEPHALUS HOLOACARDIACUS SHOWING ARREST OF DEVELOPMENT OF ALL TISSUES IN EMBRYONIC PERIOD

By BORIS BOULGAKOW, M.D.
Curator of Museums, Royal School of Medicine, Cairo

The specimen was brought from the Department of Public Health on 3rd November, 1922. This monster was born together with a female twin at full term and normally developed. The parents are Egyptians, who are in

Fig. 1.
Acephalus holoacardiacus, anterior aspect.

Fig. 2.
Acephalus holoacardiacus, posterior aspect.

good health and strong. They state that there has never been any similar case in the family. The father is a carpenter. The mother 30 years old and married since the year 1910. Her menses are usually normal. She passed through seven pregnancies; the first five children were normally developed, but they all died aged between 1 and 3 years; the sixth child, a girl, is living and is now 3 years old; the seventh pregnancy was the last and continued

9 months. During this last pregnancy, the mother felt the quickening as usual and she said that she never remarked any difference in comparison with other pregnancies except that she was "weaker" in this last one. The normal twin was born first and then the monster. The weight of the monster is about 700 gm.; all the body is covered with smooth skin. There is no head, but the head end is enlarged and rounded; on the anterior surface there is a depression bounded laterally by two folds between which there is a small gelatinous structure, representing the head. Above the depression there are a few hairs.

In the abdominal region there is an open umbilical ring, containing the umbilical cord and coils of intestines; and in the pubic region there is a structure resembling somewhat a penis. The lower extremities are well developed. The length of the monster from the upper pole to the heel is 25½ cm. Its widest diameter is 11 cm.; the inter-cristal diameter is 8½ cm. The length of left lower extremity is 12 cm. and the right 11 cm.

In consideration of the fact that the study of such a monstrosity as an acephalic holoacardiac foetus gives us a good idea as to the development of the embryo as a whole and may help us to understand and explain some difficult questions of development of different tissues, I am going to describe particularly some tissues, because they show early stages of development; the circulation, because of its going in an opposite direction to that in the normal foetus; the thoracic cavity which is empty; the abdominal and pelvic cavities for their evidences of arrest of development; and the central nervous system which shows degeneration.

THE SKIN

There is an external covering of skin and a markedly oedematous subcutaneous stratum; below this is a dense layer of adipose tissue, divided up into lobules by bands of connective tissue; under that is a layer of dense tissue resembling deep fascia. There was no evidence of hair with the exception of a few which may be seen on the upper part of the monster which represents the head. Microscopically a section from the abdominal wall is seen to contain a thin layer of epithelial cells composed of only two or three layers of cells; in this epithelium we can recognise the stratum corneum and stratum mucosum. Under this was a layer of connective tissue with a markedly oedematous Malpighian layer and subcutaneous tissue. In the second section taken from the lower limb all appearances are better shown; here may be seen the stratum corneum, lucidum, mucosum, the subcutaneous tissue, the mouths of hair follicles with the papillae and sebaceous glands in a state not fully complete; then a dense layer of adipose tissue. All structures are very oedematous and no sweat glands can be seen.

THE MUSCULATURE

The muscular system has not attained full development and is degenerated. Its appearance is not like that of normal muscle; it is difficult to recognise it from other tissues. The muscles cannot be separated because they are fused with other tissues, especially in the trunk. The muscles of the lower extremities have the same appearance, but as the tendons are well developed one can follow the direction of groups of muscles which latter cannot be separated one from the other. If a transverse section is made through such a muscle, there is seen an outer layer of muscular fibres investing layers of fatty tissue; this may be the result of fatty degeneration in the inner layers. Under the low power, fibres of muscles taken from the calf of the leg or the back of the trunk are seen widely separated, with fatty tissue filling the interspaces. Separate muscular fibres are not completely differentiated and no striation can be seen; they look more like smooth muscle fibres. Tendons and ligaments are developed in the trunk as well as in the lower extremities.

The unstriped muscle fibres in the body are developed comparatively to a high degree and thus may be recognised easily in the small intestine.

It is known that the cross-striated and smooth musculature with a few exceptions arise from the mesoderm. The cross-striated and smooth fibres are not to be considered as fundamentally different, they merely represent different grades of development, likewise different paths of differentiation from a common fundamental form.

Mareshini and Ferrari found that in the early stages of development smooth and cross-striated filaments show exactly the same structure. It has been commonly supposed that the first differentiation of the muscles from the mesoderm takes place under the influence of the nervous system through the agency of the motor nerves, and that self-differentiation of muscles does not occur. It is known that the motor nerves unite very early with the developing myotomes and muscular masses. According to Neuman's studies of acephalic and amyelic monsters, the influence of the motor nerves is necessary for the differentiation of the muscular system. Leonova has described a human monster without brain and spinal cord in which the peripheral sensory nerves and musculature were normally developed; but Weber and Neuman have described cases in which absence of certain portions of the central nervous system has been accompanied by the total absence of musculature which is normally supplied by the lacking nerves, although skeleton, blood vessels and even tendons were normally developed. Neuman would explain these apparent differences by assuming that muscles first arise under the influence of the central nervous system, but that their nourishment and further growth during the embryonic period takes place independently of the central nervous system and not until post-embryonic life is reached is the dependence again

established. Thus the nervous system must have developed in the early stages of embryonic life up to a certain point and undergone degeneration after differentiation of the muscular system had taken place.

Keibel points out that in the embryos of lower vertebrates, the connection of the motor spinal nerves with the muscle plates is established just at the time when the contractile substance begins to be laid down, but in the pig, according to Barden, the musculature is differentiated to a considerable extent before the nerves establish a connection with it.

Harrison removed the spinal cord in a series of frog embryos before the histological differentiation in either the muscular or nervous system had begun, so that isolation of the musculature from the nervous system was complete. Still the differentiation of contractile substance took place in the normal manner, as did the grouping of the fibres into individual muscles.

At how early a period in the development of the ovum this power of self-differentiation of muscular tissue begins, is problematical. In consideration of the fact that the muscular tissue in our case is slight in amount and that it has not passed through the period of differentiation, we suggest that the musculature is in an embryonic state as a result of arrest of development of the embryo. Both motor and sensory nerves are well developed and can be seen going to the muscles and periphery, supplying all tissues.

In spite of the presence of nerves to the tissues and vessels, there is no evidence of normal development, only an increase in size of muscular tissue. This suggests the idea that some organ, which should regulate the growth of muscular tissue and complete its development, is absent.

Accordingly we may agree with the suggestion of Neuman and Harrison that growth and nourishment proceed independently until the post-embryonic period begins, when dependence on the central nervous system should be established. If this does not take place, we should expect an arrest of development of muscular tissue, as is the case in the acephalus holoacardiacus we are describing.

THE CIRCULATION

The circulation of blood in acardiacus has been the subject of much discussion, particularly owing to the absence of the heart, which makes it difficult to understand how that phenomenon goes on.

Generally acardiacus is one of twins, and as it always has an umbilical cord, we may say that the deformed twin is dependent upon the placental circulation.

Before discussing the different theories of circulation in the acardiacus we will describe the complete distribution of vessels in our case.

The umbilical cord. The umbilical cord is 9 cm. in length and 4 mm. thick; it enters through the umbilical ring with coils of intestines. It looks like a

normal cord but thinner and shorter. The microscopic appearances are exhibited in fig. 3. The cross-section was taken from the middle of the cord; there is the sheath, consisting of stratified epithelium; the outer layer of cells is corneous. Within the sheath the vessels of the cord are held together by an embryonic connective tissue, Wharton's jelly. There are four vessels—two arteries and two veins. The umbilical vessels are composed almost entirely of a middle muscular coat, being simply muscular tubes; the tunica intima is rudimentary, there is no tunica adventitia, and no elastic tissue, but muscular fibres run in various directions. The outer surface of the muscular coat is seen passing into the surrounding Wharton's jelly.

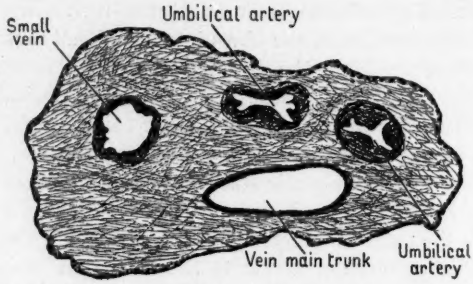


Fig. 3. Cross-section through the umbilical cord of acardiacus.

On dissection we can follow the direct path of these four vessels. The vessels were injected—one artery and one vein—in the abdominal cavity just after leaving the umbilical ring.

The X-ray photo (fig. 4) shows that the vascular system is well developed and distributed equally; there is no evidence of vessels for the liver, spleen or stomach. In the thoracic cavity only the dorsal aorta is present without any traces of the heart. We used this X-ray photo as a guide during dissection.

Fig. 5, which is schematic, shows as far as possible the distribution of vessels in different regions.

From the umbilical cord (fig. 5) two vessels pass towards the body, these are the umbilical arteries. These two vessels are seen passing on both sides of the urachus and allantois giving branches to the latter, then they give branches to the lower extremities—arteriae ischiadicae, femoralis, saphena magna—and small branches to the neighbouring structures. Arteria ischiadica is a huge vessel which arises from the lower part of the umbilical artery and runs with the sciatic nerve, which partly surrounds it. After giving branches for the thigh and knee joint it divides into anterior and posterior tibial arteries in the same manner as the popliteal artery. The femoral artery is a short vessel which goes with the femoral nerve and gives a branch, accompanying the saphenous nerve—art. saphena magna.

The umbilical arteries turn sharply backwards and when the left umbilical artery receives the right one, which latter passes behind the cloaca, the two

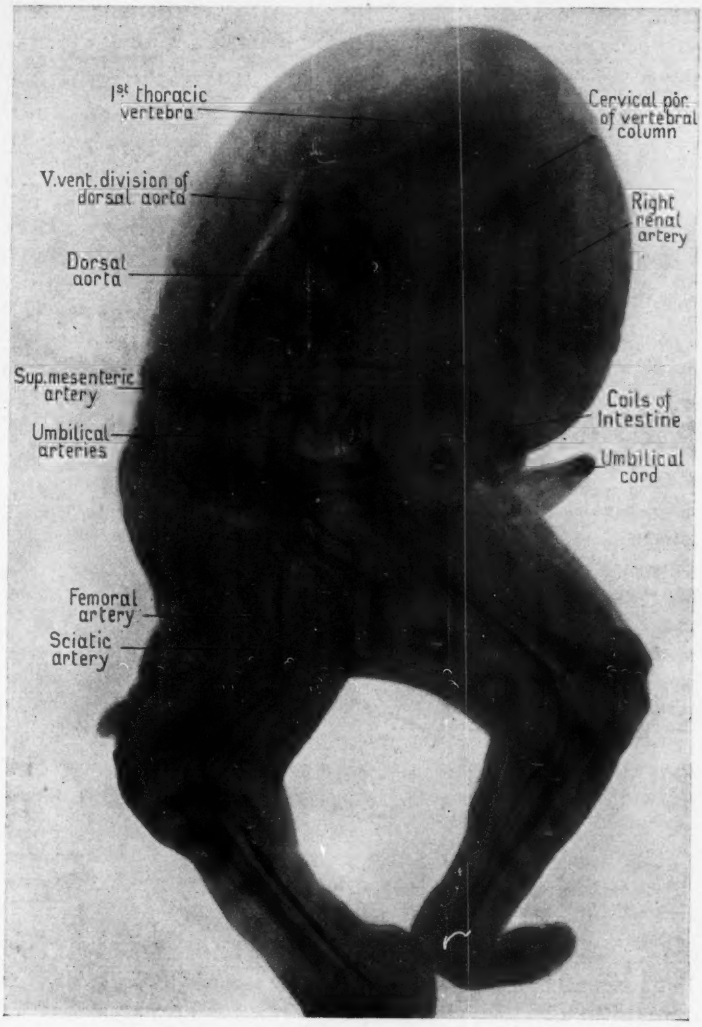


Fig. 4.

continue as one main trunk—the dorsal aorta. In its course the aorta gives branches to the large and small intestines, to the kidneys and suprarenal glands; and in its ascent it is more to the left side of the body, where it gives

intercostal arteries and ends at the level of the 5th thoracic vertebra in two big branches which diverge and pass on each side of the vertebral column. The branch of the right side passes under the clavicle of that side and then gives three small branches towards the cervical vertebrae and towards the head end of the body; then the main artery ends on the dorsal aspect of the first thoracic vertebra just under the skin; the branch of the left side takes

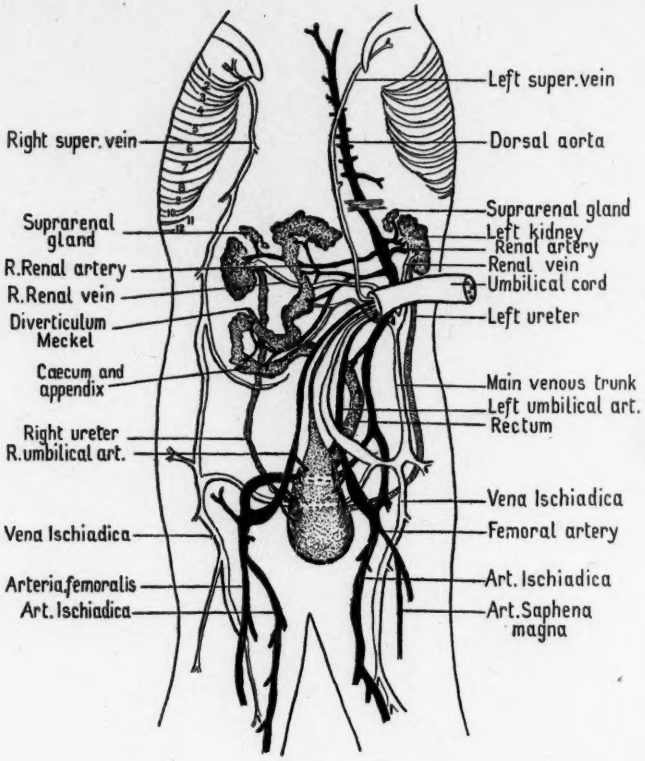


Fig. 5.

the same course and gives the same branches and, when it ends dorsal to the first thoracic vertebra, anastomoses with its fellow of the right side (fig. 6).

Towards the alimentary canal the superior and inferior mesenteric arteries spring from the aorta, but there is no trace of coeliac artery. The superior mesenteric artery, after arising from the aorta, goes directly to Meckel's diverticulum and sends a branch towards the caecum and appendix. The inferior mesenteric supplies the lower region of the large intestines and gives a big superior haemorrhoidal branch (fig. 7).

We will now describe the return of blood from the body to the umbilical cord. On the left side from above a vessel carries blood from the intercostal spaces and left side of the head end directly to the umbilical cord. See fig. 5. On the right side another vessel carries blood downwards and unites with a transverse vessel from the region of the umbilical ring; it continues downwards and, receiving the right sciatic and femoral veins, goes behind the cloaca in order to join the main vein, which latter is formed by union of the left sciatic and femoral veins from the lower extremity with the vessels of the abdominal and pelvic cavities (renal and mesenteric veins), then the main vein trunk goes towards the umbilical cord.

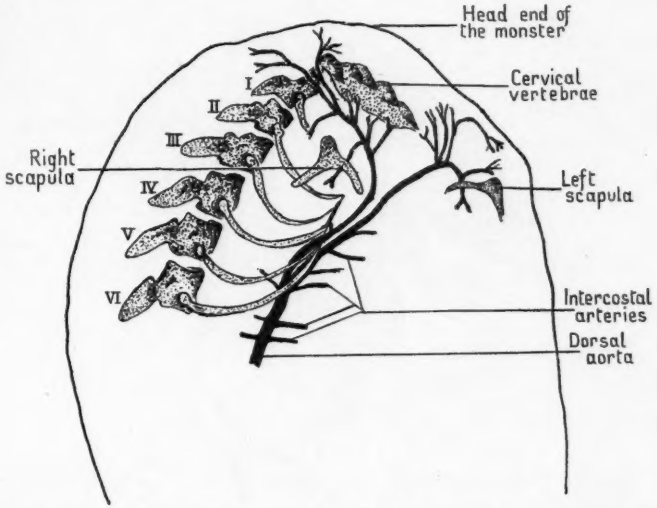


Fig. 6. Division of dorsal aorta at the level of 5th thoracic vertebra and distribution of vessels near the head end.

Now, following the distribution and positions of the different vessels, we can judge which of them carry blood from the placenta to the body and which carry it back. In the intercostal spaces every branch arising from the dorsal aorta lies between an upper vessel and a lower nerve; the upper vessel does not contain the injection mass. It is a venous vessel and it carries blood towards the placenta.

From the dorsal aorta there are two branches going to each kidney; below the branch to the kidney and between it and the ureter there is a vessel, which by its position and formation in the hylum should take blood from the kidney and carry it to the umbilical cord. It is, I suggest, a renal vein which joins with the main venous trunk (fig. 5). During injection of the main vein we found that the injection mass ran only to the big vessels of the abdominal

cavity and those of the lower extremities; but all the superficial vessels and those which carry blood from the upper part of the body were not injected. Thus we can never imagine that this vessel—main vein—could supply the whole body. On the other hand, on injecting the umbilical artery the injection substance flowed absolutely freely in different directions and filled all peripheral branches and reached every organ and tissue.

Accordingly we can say with certainty that the circulation was flowing in a direction opposite to normal, *i.e.* through the umbilical arteries to the body and through the veins to the placenta; but these veins should not be called umbilical, but vitelline veins. Probably the circulation was going on

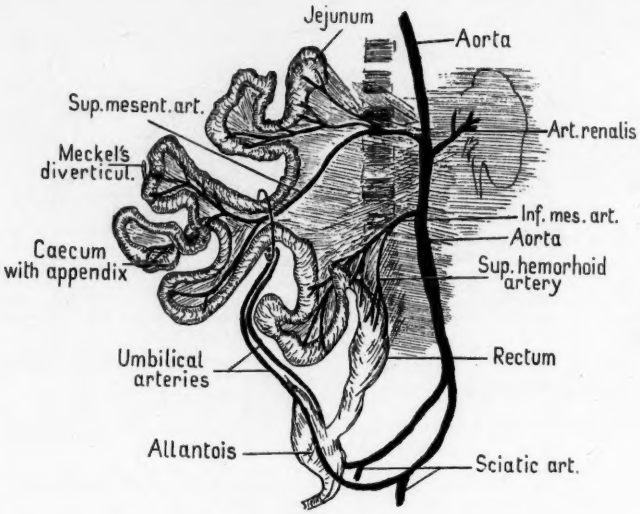


Fig. 7.

through the anastomoses of the umbilical arteries of the monster with the branches of the umbilical artery of the main twin. According to this condition, the heart of the normal twin should be recognised as the propelling agent and the deformed twin is dependent upon the placental circulation of the normal co-twin. The veins of the monster join with branches of the umbilical vein of the normal co-twin in the placenta. F. Schatz in a schematic figure explains the course of the circulation, in this way the vessels of the monster taking origin by anastomoses with the placental vessels of the normal twin (Fig. 8).

The umbilical vein itself of the monster did not develop and I suggest that the veins of the monster are the remainder of the omphalo-mesenteric veins. The vessels of the umbilical cord of these monsters are usually defective and communicate with those of the cord of the normal twin. In rare

cases, as Keibel points out, the omphalo-mesenteric or vitelline vessels may be found in the cord of the full-time foetus and be seen passing to a persistent umbilical vesicle on the foetal surface of the placenta.

In a case recorded by Ballantyne four additional vessels were found in the umbilical cord besides normal vessels and they apparently were carrying blood up to the time of birth. In another place he says that "the part played by the umbilical vesicle or yolk-sac in the nutrition of the human foetus is apparently not great. At any rate it can only be of use to the foetus in the early weeks of foetal life." In these early weeks the true yolk-sac therefore

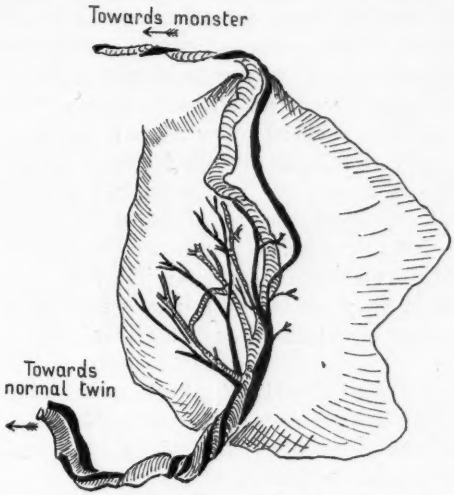


Fig. 8. Placental circulation in a case of acephalus described by F. Schatz.

is probably a source of supply to the organism in the transition period of neofoetal life, if not later. In another place he writes that

in foetuses of other vertebrates, the yolk-sac plays a very important nutritive function, but in mammals it is to all intents of no consequence as a direct source of food supply, although in some mammals it takes part in the nutrition of the foetus. In the Rodentia, Insectivora and Cheiroptera the umbilical vesicle becomes united by its vessels (vitelline or omphalo-mesenteric) with the diplo-trophoblast (Hubrecht) or subzonal membrane plus epiblast, to form a temporary structure connecting the mother with the foetus—the vitelline or omphaloid placenta. I have elsewhere shown reason for supposing that sometimes at least a vitelline placenta may intrude itself into the embryological history of the human foetus, that in the sympodical monstrosity, and possibly in other terata as well, the allantoic vessels do not develop, and yet a placenta is grown, which carries blood to the foetus to the full term of gestation, and that this placenta is formed by the vascularisation of the chorion by the vitelline vessels.

In our case we have apparently evidence of vascularisation of the chorion by the vitelline vessels, due to arrest in development of vessels and they are still not replaced by permanent ones; as evidence of this we have the presence of four vessels in the umbilical cord (two arteries and two veins); persistence of embryonic vessels like arteria and vena ischiadica; and absence of systema venae portae and vena cava inferior. From this we conclude that the embryonic circulation still persists in acardiacus.

It may be that according to Ahfeld's theory the twins developed from a single ovum and were growing in one sac and the allantois of one twin grew out earlier than that of the other (fig. 9 *a*), and that the predominant twin obtained a larger area of chorion by attachment of its allantoic vessels. In fig. 9 *b* the allantois of the predominant twin has obtained all the chorion and its vessels are united with the vessels of the monster. In fig. 9 *c* is shown the circulation, which is already established; the blood from the predominant twin passes through the umbilical artery to the monster.

This forms a good working hypothesis for the origin of the circulation in such monstrosities as acardiacus. It is possible that in consequence of the absence of space in the chorion for attachment of the allantoic vessels of the deformed twin—that the umbilical vein cannot be established directly from the placenta, but the umbilical arteries can join with the vessels of the predominant partner in the placenta itself. In such manner the malformed twin remains alive by getting blood through the placental circulation which is common to both.

If it is assumed that the blood is going to the monster through the umbilical arteries, there ought to be some veins through which blood could be carried away to the placenta; these veins I consider are the remains of embryonic vitelline veins, which join in the placenta.

In conclusion we may say that in our case of holoacardiacus acephalus we have evidence that the blood circulated in an opposite direction to the normal foetus, due to the arrest in development of the embryo at an early stage, when the embryonic vessels had not been replaced by permanent ones.

THE SKELETON

The skeleton in this monster consists of the following structures: the vertebral column, the ribs, the scapulae, the clavicles, the episternum, the pelvic bones and bones of the lower extremities. The vertebral column is normal with the exception of the cervical vertebrae, which are fused together into one mass which is bent and appears anterior to the thorax, the spinous processes of this fused mass are flattened and attached to one another. The canal is very narrow. The thoracic vertebrae are well developed and we can distinguish in each vertebra all its constituent parts. The ligaments which join these vertebrae together are well developed and these thoracic vertebrae are joined to the cervical ones by means of the supraspinal ligament. In the

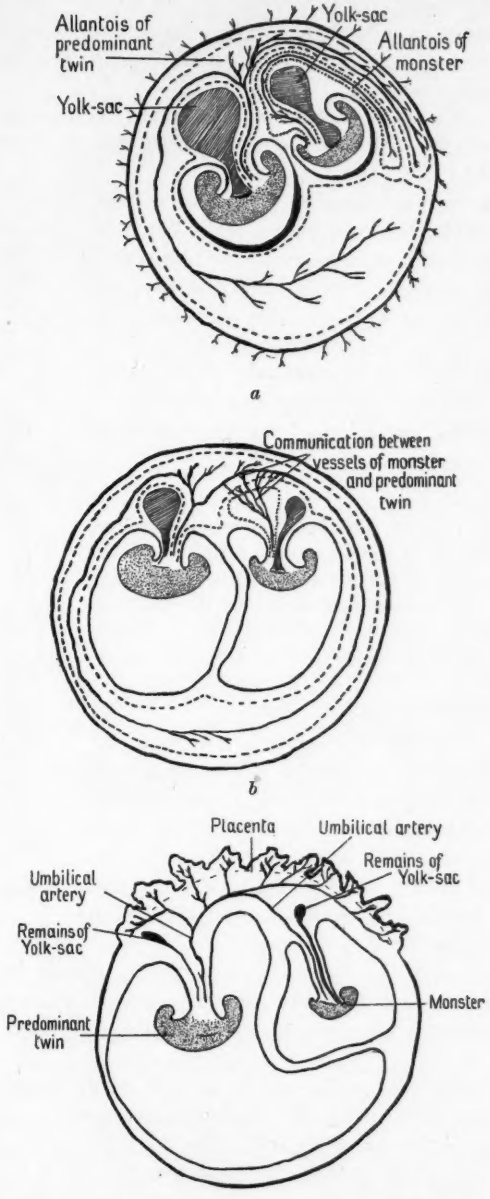


Fig. 9 *a, b, c.* **Schematic drawing explaining Ahfeld's theory of circulation in acardiacus.**

lumbar region there are five vertebrae, the lowest of which is slightly deformed. The sacrum is not completely developed and owing to the absence of the spinous processes the canal is left open; the coccyx is represented by a small cartilaginous structure.

In the thoracic and lumbar vertebrae and in the sacrum the primary centres of ossification are present, one in the body and two in the arches.

There are twelve pairs of ribs. Commencing from the 9th rib upwards, the ribs of one side join one another at their sternal ends by means of connective tissue and only in the uppermost part the first rib joins its fellow of the opposite side by means of cartilage. The sternum is not developed; the clavicles are seen directed to the episternum, the cartilaginous structure where the first ribs of opposite sides meet.

All ribs with the exception of the 1st, 11th and 12th have primary centres of ossification.

Keibel says:

> The sternal ends of the clavicles become united with one another by a dense band of tissue, which probably represents the episternum of lower forms and later when the heart has descended into the thoracic cavity, the cranial ends of the sternal plates become united with one another, and the episternal band becomes united to them and loses its intimate connection with clavicles.

Fig. 10.
The skeleton of acardiacus.

Of the upper extremities only the scapulae and clavicles are developed and these are cartilaginous in structure. The scapulae are situated at the level of the first two thoracic vertebrae. From the upper and anterior angle of the scapula arises the acromion process, the continuation of which is the clavicle. The vertebral border of scapula is concave, and in the axillary border there is a small incisura which would have been the socket of the humerus; the coracoid is not present. Nearly the same position and outlines of the clavicles and scapulae are described by Keibel in an 11 mm. embryo. Compare fig. 11 with fig. 12 taken from Keibel's *Embryology*.

The constituent bones of the pelvis are well developed and are normally ossified. In the lower extremities the bones are nearly complete with the exception of some of those of the feet. The two extremities of the femur are fully formed; the shaft of the left femur was fractured accidentally. The shaft is ossified and the secondary centre for the lower end is present. Normally ossification begins in the middle of the shaft at the 7th week of

foetal life, but the secondary centre appears during the 9th month. The shafts of the tibia and fibula are ossified. The patella is still cartilaginous.

In the left foot the calcaneus, talus, cuboideum, lunatum, and two cuneiform bones, three metatarsal bones and five phalanges are present. The 1st

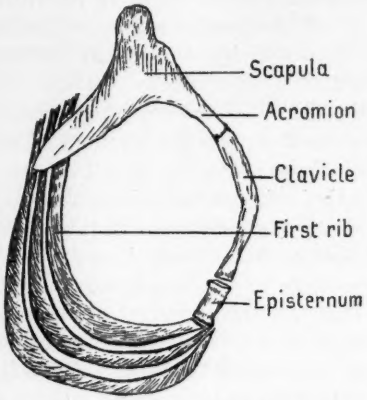


Fig. 11. The scapula with acromion, clavicle and episternum of acardiacus.

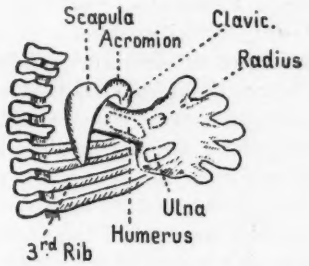


Fig. 12. The skeleton of the superior extremity in 11 mm. embryo. Keibel.

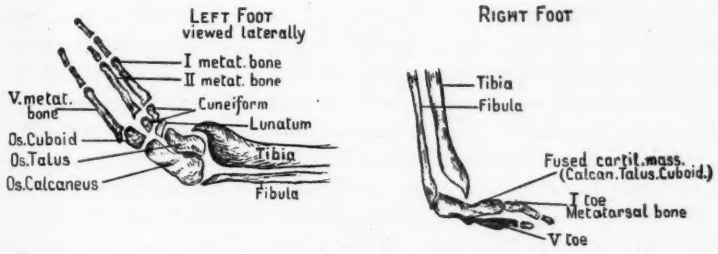


Fig. 13.

and 5th toes are nearly complete; the 2nd toe has only a metatarsal bone with one phalanx. There is a centre of ossification only in the calcaneus. In the metatarsal bones and in the phalanges the shafts are ossified.

The right foot is less developed; there is one fused cartilaginous mass instead of the talus, calcaneus and cuboid bones; two metatarsal bones for the 1st and 5th toes and two phalanges. The shafts of the two metatarsal bones and the two phalanges are ossified.

Looking at the skeleton as a whole one can see that the bones of the skull are entirely undeveloped; the vertebral column is developed to a certain extent. The thorax is closed only at the region of union of the first two ribs; the sternum is undeveloped; the upper extremities are represented only by

the clavicles and scapulae. All these evidences resemble structures which are seen in the embryo. Besides this, the lower extremities show pes varus, which should be regarded as a congenital abnormality. The limbs are disposed in a natural attitude of flexion *in utero* and the feet are so placed as to look as if there was pes varus, but there is of course no real club foot. In regard to congenital club foot, this defect very frequently occurs and is associated with other malformations. It is due to interference with development, but also may be due to mechanical conditions acting upon the growth of the extremities, such as insufficient room in the uterus or deficiency of amniotic fluid. Pathological conditions which produce these peculiar positions of the lower extremities must be considered, as well as contraction of soft tissues—muscular, tendinous or fascial; or degenerations of bones and joints. Probably these pathological conditions are the result of congenital defect in the central nervous system (absence of brain and degeneration of spinal cord), which caused the muscles, tendons and fasciae not to be developed, being unable to act upon the extremities as usual. This appearance should be regarded not as an arrest of development of the skeleton but as secondary to the mal-development of the above-mentioned tissues. On the other hand, if we examine centres of ossification, we can see that the process of ossification was going on normally, i.e. in those bones, where all primary centres should appear during foetal life, these centres may be seen present, in spite of the degeneration of the spinal cord and the absence of the brain with the pituitary body. Accordingly we suggest that there was no influence of the central nervous system acting upon the growth of bones during foetal life, and the absence of the pituitary body did not prevent the growth.

With reference to the absence of the influence of the central nervous system upon the growth and development of osseous tissue, I wish to allude to the nourishment of this tissue, which is well developed. It is possible here that the most important rôle in the development of osseous tissue was fulfilled by the normal blood supply, regulated by the action of trophic nerves penetrating into the bones together with the vessels. In our case the sympathetic system is present, as we proved by microscopical examination of the suprarenal glands; in these sections the sympathetic ganglia are well developed, and during dissection there were found some nerve fibres, which formed the renal plexus, from which nerves could be seen directed to the vessels. It is well known that when there is injury in the spinal nerves—primary atrophy in bones does not occur, but only secondarily, as a result of the absence of the normal pull of the muscles.

In conclusion, I suggest that the bones increased in size without developing into a complete skeleton, because there was no brain which could regulate development. In our case the skeleton of acardiacus continued to increase in size from the time when development of the embryo was arrested—about 4th–5th week.

THE THORACIC CAVITY

The cavity is full of a jelly-like tissue; there was no evidence of any organ (heart, lungs or oesophagus, etc.).

For microscopical examination sections were taken from different places, but everywhere the appearances were the same. In the section is seen connective tissue in an embryonic state with cells and a few capillary vessels. Between thoracic and abdominal cavities there is a septum transversum consisting of fibrous filaments of connective tissue.

ABDOMINAL CAVITY

In the abdominal region, 5 cm. above the pubis, is the deficient umbilical ring, through which the umbilical cord is seen passing and some coils of intestines protruding. The subcutaneous tissue of the abdominal wall as elsewhere is oedematous and is blended with the deep fascia and muscles to form one fused mass from which the muscles cannot be separated. Under the microscope the muscular fibres were seen to be of the non-striated type and ran in different directions. The subcutaneous nerves are present.

The coils of intestine, which lie in the umbilical aperture, belong to the small and large bowel; this is clear from the presence of Meckel's diverticulum and caecum with appendix. The intestines are covered as a whole with peritoneum and represent one big intestinal loop with the mesentery, which latter goes to the posterior wall of the abdominal cavity. When the abdominal cavity was opened the following structures were found: the small and large intestines with the rectum, the kidneys with the suprarenal glands, genital organs and in the middle the allantois with cloaca to which the rectum is attached. On both sides of the rectum are the ureters in connection with the Wolffian ducts. Stomach, duodenum, liver, pancreas and spleen are wanting. On opening the cloaca one can see by the naked eye the openings of rectum, ureters and Wolffian ducts in the cavity (fig. 14).

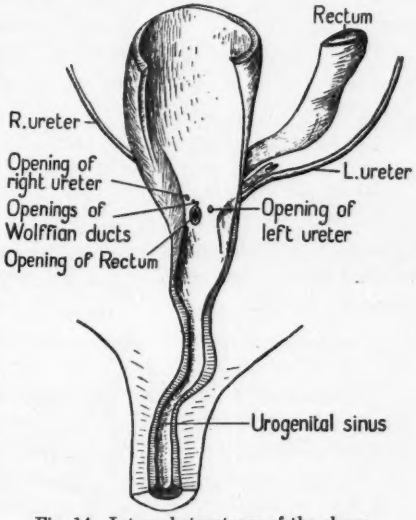


Fig. 14. Internal structures of the cloaca and urogenital sinus.

Anteriorly the cloaca continues as the sinus urogenitalis (fig. 15), which projects forwards and beneath the pubis like a penis. This latter is 1·5 cm.

in length and 11 mm. in thickness and its external aperture is closed by the urogenital membrane. The intestinal tract begins blindly at the level of the 10th thoracic vertebra in the right side. This upper end is distended and its internal surface is folded; this part from its microscopical structure may be considered as jejunum.

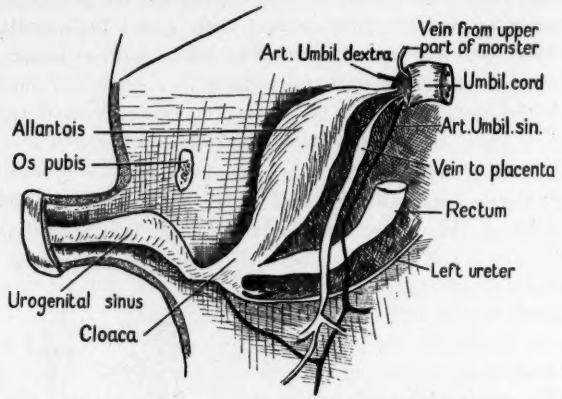


Fig 15. Schematic drawing of the cloaca of acardiacus showing earlier embryonic stage of development than in Keibel's model of human embryo from eight and a half to nine weeks old.

In fig. 16 one can see that the wall of the intestine is composed of the epithelium covering the internal surface and the mucous membrane which projects above the surface as the villi. The mucous membrane contains simple vertical gland tubes—the crypts of Lieberkuhn; the mucosal and submucosal muscular layers.

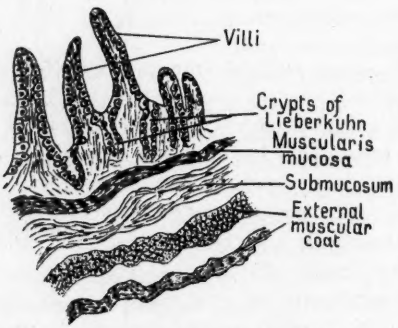


Fig. 16. Section from uppermost part of jejunum.

In spite of the presence of all histological structures, the constituent tissues are not highly developed. Microscopical appearances of the large intestines are normal, but still they are like young tissue. The appendix looks like a continuation of the caecum. All the intestinal tract is 39 cm. in length;

at a distance of 13·5 cm. from the blind beginning of the small intestine is Meckel's diverticulum with the superior mesenteric artery, which goes directly to this intestinal part, and at a distance of 18·5 cm. is the caecum. There is no evidence of rotation of the large intestine, and the whole intestinal tube is attached by a primary mesentery. The large intestine ends as the rectum, which latter is ampullated before it joins the cloaca.

On each side of the vertebral column there is a kidney at the level between the 10th thoracic and 2nd lumbar vertebrae, with the suprarenal glands above; the kidneys are brown in colour, deeply lobulated and not of the same size. Left kidney is 2·5 cm. in length, 1·8 cm. in breadth and 0·9 cm. in thickness. The right is 1·9 cm. in length, 1 cm. in breadth and 0·9 cm. in thickness.

The kidneys are lying under the peritoneum and are covered with capsules containing a lot of fat. The ureters enter the hylum below the vessels; the

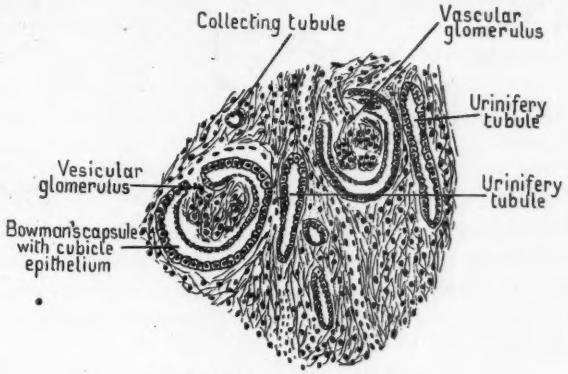


Fig. 17. Kidney of acardiacus.

left ureter descends almost straight, but the right one is slightly sinuous. The kidneys are placed in such a manner that the hylum looks anteriorly. In relation to neighbouring structures the coils of the small intestine are seen lying upon the right kidney; the large intestine rests upon the anterior surface of the left kidney. The lobulation is better marked in the right kidney than in the left. In section the kidney shows the structure of a very young organ with lobules separated by deep interspaces, and each lobule contains a separated pyramid. Peripherally there is a cortical layer overlying a medullary layer. Microscopically one can easily see the well-developed Malpighian corpuscles. The internal wall of Bowman's capsule is lined with a thin layer of cubical (fig. 17) epithelium, which latter is reflected as cylindrical epithelium to line the external wall of the capsule. Inside the Malpighian corpuscles there is seen the vascular glomerulus, infiltrated with round cells. Uriniferous tubules and collecting tubules may be seen under the microscope (fig. 17). From the position and structure of the kidneys they appear to be

in an early stage of development; this is well shown by Bowman's capsule, whose external wall in the adult and in the normal child is covered with flat epithelium while the internal wall is like a very thin cuticular layer. Besides, if we compare this with the normal kidney in the adult we find that in our case the uriniferous tubules are only slightly developed and few in number.

The ureters are present at the end of the 4th week of embryonic life as a small bud attached to the Wolffian duct just above its opening into the cloaca. In the 5th week this bud develops a stalk and becomes the permanent kidney and duct (ureter), which lie in the lumbar region.

In conclusion, knowing that the kidneys with ureters are present in the embryo about 4th–5th week and observing the similarity between appearances of a normal embryonic kidney and those in our case, we suggest that

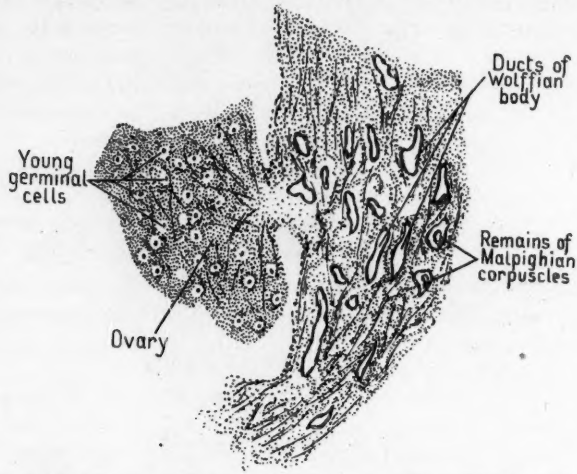


Fig. 18. Cross-section though the ovary and remainder of Wolffian body.

there is increase in size of an organ, i.e. growth without corresponding development. Thus here we have arrest of development caused, as I suggest, by absence of a regulating organ—the central nervous system.

Above each kidney there is the suprarenal gland, which under the microscope is seen in the developing stage, but there one can see the zona glomerulosa, fasciculata and reticularis slightly degenerated. Besides these suprarenal structures, there are seen in the section the sympathetic gangliae with big medullary cells.

On each side of the abdominal cavity there is a small organ $\frac{1}{2}$ cm. in diameter, resembling the ovary. Under the microscope one can easily judge that they are ovaries in an early embryonic stage of development, containing large germinal cells (primitive ova), remainder of Malpighian corpuscles and Wolffian ducts. According to Nagel, at the 5th week it is possible to determine

by microscopical examination whether the genital gland is male or female; if it is to be an ovary the large germinal cells (primitive ova) are numerous and the germinal or coelomic epithelium forms a thick layer of several rows of cells.

In the pelvic cavity there is the allantois which continues upwards as the urachus. The length of these structures is 4·5 cm.; the widest diameter of the allantois is 2·5 cm., its walls are smooth, and the infero-posterior part is thick, forming the cloacal floor. Anteriorly the cloacal cavity continues as a canal (urogenital sinus) below the pubis and it ends blindly, being closed by the urogenital membrane. The length of the urogenital canal, counting from the cloacal cavity, is 4 cm.; this canal in its further development is transformed into the urethra and vagina if the future child is to be female. The same state of development of organs in the abdominal and pelvic cavities is described by Ballantyne in his account of a normal embryo in the 4th week.

According to Hertvig, just before the Wolffian duct enters the cloaca, a small blind tube arises from it and is converted into the ureter and kidney. This blind tube appears during the 4th week after impregnation.

All these appearances, as the state of deficient abdominal wall, the protruding intestines with their relation to the peritoneum, the state of cloaca, and the state of development of kidney tissue and genital glands, show that in our case we have arrest of development of an embryo in a very early stage, the organs having increased in size without corresponding development due to the absence of the regulating organ—the central nervous system—and that arrest has taken place about the 4th–5th week after impregnation.

NERVOUS SYSTEM

Peripheral nerves. During dissection it was seen that the peripheral nerves were distributed as sensory and motor, and it was recognised that these nerves reached the skin and muscles in all parts which are well developed. Schwalbe mentions that the peripheral nerves are present even if the central nervous system is missing, but these nerves are developed in correlation with de veloping parts.

Microscopical examination of a cross-section of the sciatic nerve shows the following structure: the perineurium as a sheath for the individual nerve bundles; the epineurium, consisting of bundles of connective tissue fibres and containing many vascular trunks cut transversely; nerve fibres composing the nerve bundles are seen as irregular circles which are embedded in endoneurium containing numerous nuclei which belong to the connective tissue cells. The nerves directed to the lower extremities are connected together to form plexuses as usual (the ilio-lumbar, sacral, coccygeal) but before joining the spinal cord they become very attenuated.

Tiedemann in describing a case of acephalus holoacardiacus writes that the nervous system of this monster consisted of the lower part of the spinal cord which began as a ligament in the upper part of the vertebral column. The

lumbar nerves escaped from the spinal cord in a normal condition. The sympathetic nervous system began at the level of the 5th lumbar vertebra and formed the renal plexus with medullary ganglia, from which the nerves were directed to the kidneys.

In our case the main group of sympathetic ganglia is near the suprarenal glands, from where nerve filaments are directed to the kidneys as renal plexuses, and to the vessels.

THE CENTRAL NERVOUS SYSTEM

The central nervous system is very incompletely developed; the brain is absent; in place of the head there is a structure composed of cartilaginous tissue, skin with all adjacent glands and hair, but there is no evidence of nervous tissue. This structure may be called the head of the monster because it seems to be lying on the cervical part of the vertebral column, and besides there are well-developed hairs on its uppermost part.

After removing the vertebral arches and opening the dura mater one can see the spinal cord covered with arachnoid and pia mater. On both sides of the spinal cord there are seen 22 nerve roots and ligamenta denticulata. The length of spinal cord is 10·5 cm.; it begins at the level of the 1st thoracic vertebra, like a ligament composed only of the membranes, and reaches the middle of the body of the 3rd lumbar vertebra, continuing downwards as the filum terminale, which is attached to the end of the sacrum. The nerve roots which arise on both sides of the spinal cord are directed in its upper part upwards, in its middle part horizontally and in the lower downwards (fig. 19).

Fig. 19. Spinal cord of the acardiacus.

This evidence shows that the spinal cord stopped development while the vertebral column continued to grow or the spinal cord may have undergone degeneration before it attained complete development. In cross-section the spinal cord appears flattened. Microscopically, a cross-section of the spinal cord taken between two nerve roots at the level of the 5th thoracic vertebra, shows that the central canal is near the anterior surface, and posterior to the canal the medullary substance is degenerated and consists of detritus. The grey matter is not yet differentiated and it is impossible to distinguish it from white matter. Ballantyne says that during the 4th week of embryonic life a beginning is made with the differentiation of the cord into a grey and white part, but as yet there is no contrast in colour, for the medullary sheaths of the nerves do not appear till the 5th month of antenatal life.

Furthermore in our section large cells with outgrowths directed to the periphery are seen in every part (fig. 20).

According to the above-mentioned facts the central nervous system is in a condition of mal-development (absence of brain and degeneration of spinal cord), thus its influence upon the development of the body was either absent or only functioned to a very slight extent.

It is known that all parts of the organism are laid down in embryonic life and in future should grow up and take their normal appearance. This applies to the central nervous system as well as all other parts of the body and it completes its development just at the beginning of foetal life; thus if we suggest that it has an influence upon the development of the organism,

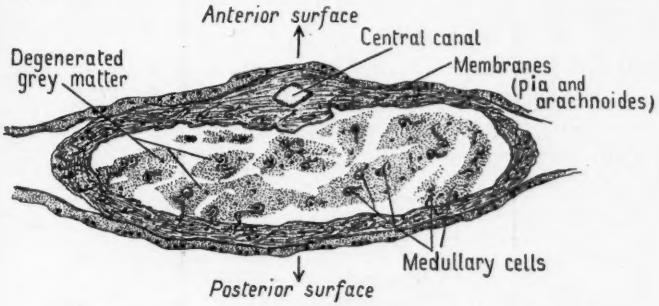


Fig. 20. Cross-section through the spinal cord of the acardiacus.

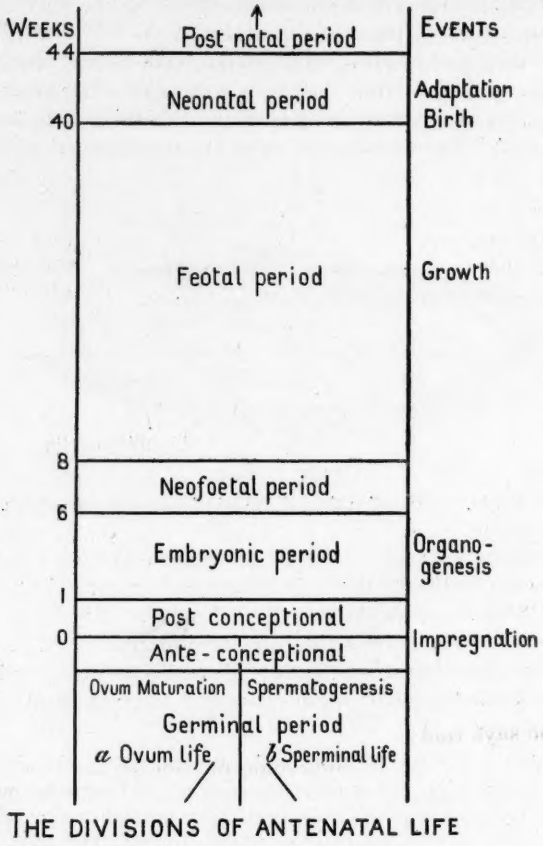
leading the latter to its complete state, there should be a connection between it and other parts; therefore if this influence does not exist, all the organs are left to their own efforts for growth and consequently there will be arrest of development. Ballantyne divides the intra-uterine life of the embryo and foetus into the following stages: embryonic period (organogenesis), neo-foetal period, foetal period (growth), neo-natal period and post-natal period (fig. 21). and he says that:

in embryonic life the embryonic physiology has not to do with organs and their special activities, but with the special activity, which produces, builds up, and perfects the organs themselves. The great function of the embryo is to form tissues and organs, or in one word it is organogenesis.

In another place he says:

we have to imagine an aggregate of cells arranging themselves, apparently in a disorderly fashion or in a fashion of which the order is but dimly discerned, first into the three layers of the blastoderm and then after many intermediate stages and phases into the organs which take on the particular functions of foetal and post-natal life. It can be recognised that the principal manifestation of embryonic life stands out prominently as organogenesis, while the chief sign of foetal life is the functional activity of the various organs, which go to constitute the foetal economy.

If this is correct there should be a regulator for the functioning and development of all organs, which I suggest is the central nervous system. If conditions are such as we have in our case, then tissues and organs would only continue in growth with the same appearances in which they were laid down, assuming that there is a good blood supply. The idea that the central



THE DIVISIONS OF ANTENATAL LIFE

Fig. 21.

nervous system, particularly the spinal cord, is the centre of regulation and formation of all parts of the organism, is not new—it was proposed and supported by many authors (Daresté and others). They tried to prove this by facts; for example, the absence of the olfactory nerves in cyclopia, in which there is often no nose to be found, or the unilateral atrophy of the spinal cord, which leads to congenital absence of one limb Harvey tries to explain hare-lip and cleft-palate or ectopia cordis as evidences of arrest of develop-

ment. Apart from these facts some embryonic structures persist to a later stage; for example, the aortic arches, or urinary fistula from the persistence of the urachus. Sometimes some structures, which should become rudimentary in the foetal period, remain as malformations by excess as when the Müllerian ducts in the male suffer an arrest in their process of disappearance and are found as Fallopian tubes and uterus in addition to the male genital organs, as for example in hermaphroditus spurius.

Of such examples, showing the different evidences of arrest of development, we can give many, but they do not allow us to arrive at a conclusion, because they appear in different kinds of monstrosities and, as Ballantyne says, this explanation, *i.e.* the influence of the central nervous system, fails and other modes of origin must be adduced. But if we will examine our monster acephalus holoacardiacus, we can find according to what already has been said above, that there are evidences of arrest in development of all tissues and organs, and that they keep the character of the early embryonic stage before the central nervous system has begun to exercise its control. The objection of Ballantyne, that the presence of many organs and parts in the placental parasite twins (acardiacus) which have no brain or spinal cord seemed to tell against the influence of the central nervous system upon development, does not invalidate my suggestion as to the arrest of development, caused by absence of the brain and degeneration of the spinal cord, because in such monsters as acardiacus, although it is true that many organs are present, as I have proved microscopically, all the tissues and organs are in an embryonic stage and they are only enlarged in size without further development.

Another objection has been raised against the influence of the central nervous system in such monsters as anencephalus, where there is no brain, but the foetal tissues are advanced in development. As many authors suggest, this anencephalic condition may be due to the presence of amniotic adhesions, or to hydrocephalus, which is the more widely accepted theory. In regard to this theory we find descriptions by Markot, Morgagni, Tiedeman and Ryan, the last of whom writes:

> It is easy to understand that the serosity, or water, as it is improperly called, may distend the brain, rupture its membranes, separate the bones of the cranium, burst the scalp and finally escape into the amniotic fluid. The whole brain, membranes, bones and scalp are destroyed by absorption, and the base of the skull alone remains, forming the anencephaly.

In another place he states that: "hydrocephalus may advance rapidly, burst the cranium and produce anencephaly or microcephaly."

J. Y. Simpson states that the malformation in an anencephalic monster arises from disease in intra-uterine life, namely, from bursting of the head when hydrocephalic.

Accepting as a fact that the anencephalic foetus is probably a result of

hydrocephalus, I suggest that anencephalus may take place after the time of embryonic development when all organs have been laid down.

In reference to this Taruffi says that anencephalus cannot take place earlier than the 4th–5th week after impregnation, for the reason that there are often well-formed eyes, but the eyes are not independent of the part of the brain which is destroyed. Alfred W. Hughes (*Lancet*, 1887) found great difficulties in explaining the fact that eyes with the optic nerves were developed, although only parts forming the posterior vesicle were present, therefore he thought that all the vesicles at one time had been present and underwent a certain degree of development, which afterwards became aborted, and gave place to retrogressive changes.

Thus the presence of well-developed parts of the face in an anencephalic monster does not oppose the fact that the central nervous system must be the regulator during foetal development, because anencephalus may take place during or after the transition period, when the placental circulation is established. If we suggest that anencephalus is due to preceding hydrocephalus, which latter is self-cured by the bursting of the head and escape of the liquid into the amniotic sac, then the remainder of the brain with the spinal cord may take on the control of development. Such a monster can develop and grow because a part of the central nervous system is present and placental circulation is established. Daresté is strongly of opinion that the dominating factor is the defective state of the brain and that the facial and other malformations follow upon this.

Therefore the idea that the arrest of development of an embryo as a whole is a result of absence or destruction of the central nervous sytem, which should play the rôle of regulator during foetal life, is quite probable.

SUMMARY

In the anencephalic monster, as described above, the brain is absent and the spinal cord is degenerated, therefore there is complete arrest of development due to lack of its influence, but growth without development continues. This is shown in the following facts:

(1) The muscular system has not attained full development and separate muscle fibres are not completely differentiated and no striation can be seen; the appearance resembling smooth muscle fibres.

(2) The blood circulates in an opposite direction to the normal foetus, and embryonic vessels have not been replaced by permanent ones.

(3) The skeleton continues to increase in size from the time when the development of the embryo was arrested at about the 4th to 5th week. In this connection the absence of the pituitary body did not prevent the growth of bones and all centres of ossification are present.

(4) In the thoracic cavity no organs are present; the space being fully occupied by embryonic tissue.

(5) In the abdominal cavity, the stomach, duodenum, liver, pancreas, and

spleen are absent; the intestinal canal begins as the jejunum and ends as the rectum opening into the cloaca with the Wolffian ducts and ureters. The kidneys as well as genital glands show the arrest of development in a very early stage, being increased in size without corresponding development, and in every respect resemble the embryonic organs.

DEDUCTIONS

1. This monster belongs to the type anencephalus holoacardiacus (omphaloangiopagus twins).

2. The arrest of development of all parts of the organism is a result of absence of the influence of the central nervous system during foetal life.

3. During the embryonic period all parts of the organism are laid down as well as the central nervous system, but as the latter does not grow further and thus its control is stopped, then the organs and tissues remain in their present state of development and only increase in size.

4. The development of the bony tissue is not under the control of the central nervous system.

5. The pathological conditions of the ovum, or the primary injury of an embryo in the early stage of development is a main cause of such malformations as acardiacus.

I would like to thank Professor D. Derry for his great help, guidance and advice. I am indebted to him for revising and correcting the paper, and to Dr A Girgis for helping me in taking photographs and in preparing some microscopical slides.

LITERATURE

(1) Keibel, Franz and Mall, Franclin P. (1912). *Human Embryology.*
(2) Birnbaum (1912). *The malformations and congenital diseases of the foetus.*
(3) Ballantyne, I. W. (1902). *Antenatal pathology and hygiene.*
(4) Schwalbe, Ernst. *Die Morphologie der Missbildungen des Menschen und der Tiere.*
(5) Ahlfeld (1880). *Die Missbildungen des Menschen.*
(6) Taruffi. *Storia della teratol.*
(7) Tiedemann. *Anatomie der kopflosen Missgeburt.*
(8) Gladston, Reginald I. (1905). "An acardiac foetus." *Journal of Anatomy and Physiology.*

A CASE OF DICEPHALIS, DIBRACHIUS, DIPUS SHOWING CERTAIN FEATURES OF EMBRYOLOGICAL INTEREST

By SYDNEY SMITH, M.D., D.P.H.
Professor of Forensic Medicine

AND BORIS BOULGAKOW, M.D.
Curator of Museums, Royal School of Medicine, Cairo

The specimen was brought to the Medico-legal Department with a short history that it was the result of a full-time pregnancy, had been born without

Fig. 1.

difficulty and had never lived. The mother is an Egyptian about 45 years of age and had had two previous normal births, one 15 years, the other 5 years before. No abnormalities had appeared in the family of mother or father

previously. It appeared well nourished and well developed and had the appearance of a full-time foetus. Its length was 51 cm. and its weight 6·5 kilos.

Fig. 1 is a photograph and sufficiently shows the external appearance. The two heads are equally well developed, there is one trunk broader than normal, two upper and two lower extremities, one scrotum and penis and two ani. This case appears to be of sufficient interest to record for a study of the characters of doubling and it may possibly give some help in the investigation of development of different parts of the embryo and the method of fission in twin formation.

During dissection we found certain abnormalities which suggest that fission occurred in a very early stage of the blastocyst and was confined to the posterior surface of the embryo, the ventral aspect of which remained single. A study therefore of the double and single parts may indicate which structures are developed from the ventral aspect of the embryo.

DISSECTION

Circulatory System

See fig. 2, schematic figure, and fig. 3, X-ray photograph. There are two hearts joined together and enclosed in one pericardium. The heart of the right twin consists of one auricle and one ventricle communicating by a bicuspid valve. The heart of the left twin consists of two auricles connected by a foramen ovale and two ventricles arranged in a normal manner with the usual valves.

The single auricle of the right twin connects with the right auricle of the left twin by an opening 15 mm. in diameter. The three auricles therefore communicate with each other.

Vessels. There is one superior vena cava common to the two twins and this is formed from the junction of the left innominate vein and the pulmonary veins of the right twin, with the two innominate veins of the left twin, and this venous trunk enters the right auricle of the left twin.

The right internal jugular vein of the right twin passes directly to the single auricle of the right twin.

There are two inferior venae cavae; one enters the single auricle of the right twin, the other enters the right auricle of the left twin.

The pulmonary veins of the left twin enter its left auricle.

From the ventricle of the right twin arise an aorta and a pulmonary artery separated by a short muscular septum in the upper part of the ventricle which represents the division of the primitive truncus arteriosus into aorta and pulmonary artery.

The pulmonary artery of the right twin divides into three branches, one of which forms the ductus arteriosus, the others supplying the lungs of this twin.

The vessels from the heart of the left twin are arranged in the normal manner.

The circulation in the heart is therefore so arranged that blood enters the single auricle of the right twin and the right auricle of the left twin through the inferior venae cavae.

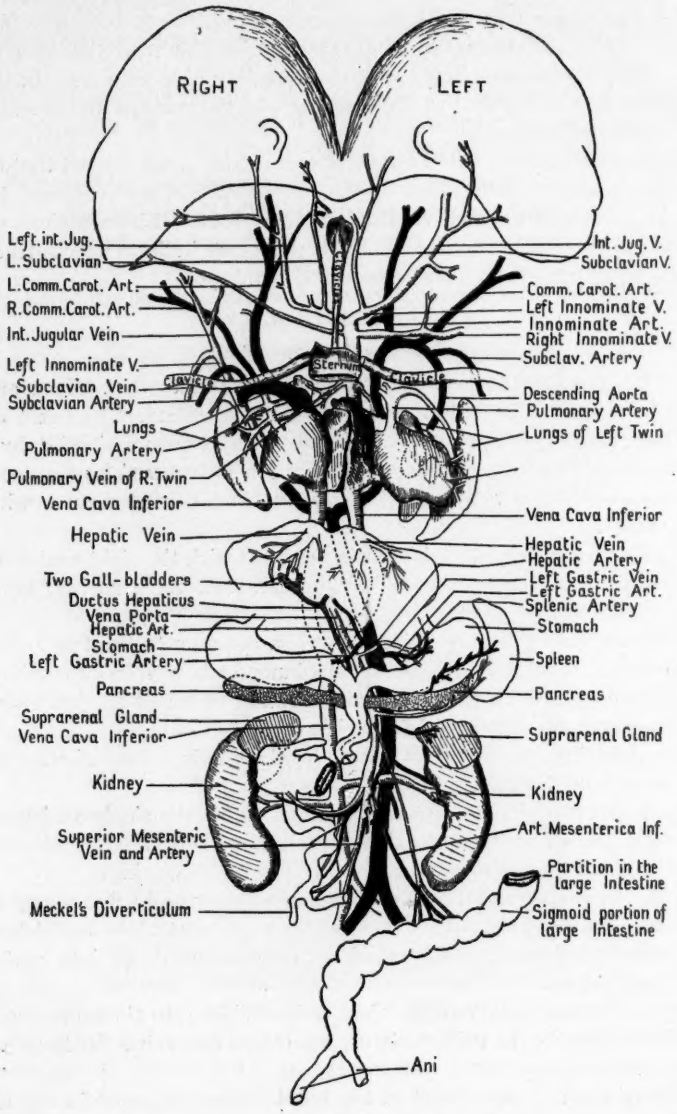


Fig. 2.

The common superior vena cava passes to the right auricle of the left twin; and into the single auricle of the right twin passes its right innominate vein.

There are two aortae, which join to form one trunk behind the liver, immediately after which two coeliac axes are given off. The left coeliac axis has the normal three branches, the right has only two, due to the absence of the right spleen.

The single abdominal vena cava splits into two at the point of junction of the two aortae, each trunk passing to its proper heart. Each vena cava receives a large hepatic vein after splitting.

Taking the circulation as a whole, doubling is seen only in the upper part of the body and continues to the point of origin of the coeliac axes.

A partial doubling is also seen in the lower part for the supply of the two ani.

This doubling of the circulatory system is intimately correlated with the doubling of the viscera, as will be described later.

There is also an interesting arrest in development in the heart of the right twin, inasmuch as the heart consists of two chambers only, and the aorta and pulmonary artery are separated by means of a short muscular septum which has stopped short of dividing the ventricle into two. The auricle, though forming one cavity, is still in the early stage in which it exhibits two lateral diverticula which should have developed into the auricular appendages.

Skeleton

The skeleton shows exactly the same appearance as that of the case of dicephalis figured in the collection of the Göttingen Women's Clinic (fig. 4 from Birbaum).

In our case there was found complete doubling of the vertebral column; in the thoracic region the two columns are joined by means of intervertebral processes which may be fused ribs.

Laterally there are 12 normal ribs on each side.

Each vertebral column contains a spinal cord.

The two vertebral columns, widely separated above, gradually incline to the middle line, and at the upper part of the sacra they are in close opposition, thereafter again sharply diverging.

The pelvis is so arranged that each sacrum articulates with one innominate bone, and with each other in the middle line.

The two lower extremities are normal in all respects.

The upper limbs are two in number and normal in development. Each articulates with a scapula and there are two clavicles attached to the sternum in a normal manner. In addition to this, in the middle line at the junction of the two necks there is a bony mass consisting of two fused scapulae and from it two fused clavicles are directed forwards and articulate with the middle of the upper border of the sternum.

Fig. 3

VISCERA

In the thoracic cavity there are two pairs of lungs; each pair consists of

Fig. 4.

one large lung situated laterally and one small situated medially (the medial lung is about one-third the size of the lateral lung).

Alimentary tract. There are two oesophagi, which incline to the middle line, pierce the diaphragm at the level of the 10th dorsal vertebra and enter the stomachs.

There are two stomachs, the pyloric ends of which are directed to the middle line, where there are two duodeni which join together in the lowest part of the descending portion, thereafter forming a single jejunum and ilium.

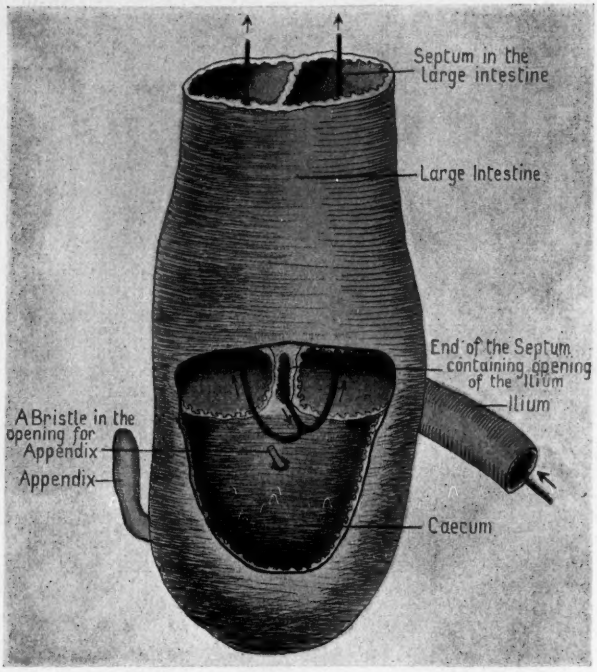


Fig. 5.

The small intestine therefore is normal except that there is a large Meckel's diverticulum.

The caecum is single and situated at the level of the right suprarenal gland, and is continuous with a single appendix.

The large intestine appeared to be a single tube, but on opening it was found to be divided into two by a longitudinal septum. The ilium joins the caecum in the middle of this septum (fig. 5). There is no ascending colon; the longitudinal septum continues along the colon as far as the perineal flexure of the rectum where the bowel divides into two separate canals which rapidly diverge to the two ani.

The liver is large and resembles two fused livers and there are two separate gall bladders the ducts of which join and pass to the lowest part of the descending portion of the duodenum.

The presence of two gall bladders and the disposition of the hepatic veins indicate that the liver is doubled (see figs. 1 and 2).

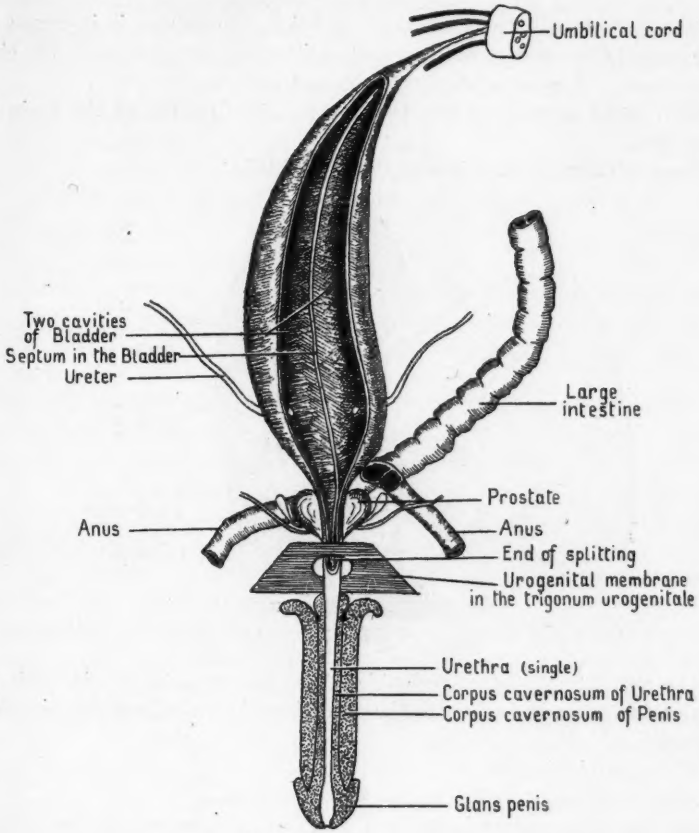


Fig. 6.

The pancreas consists of two heads fused in the middle line with the two tails directed to opposite sides.

The spleen is single and is situated behind the left stomach.

There are two kidneys, two suprarenal glands and two ureters, which open into the two sacs of the bladder. There is a single bladder divided into two distinct sacs by a mesial longitudinal septum (fig. 6) which continues to the level of the external layer of the urogenital membrane where it stops,

the pars prostatica and pars membranacea urethrae being therefore doubled. A single urethra continues from this point and passes through the corpus cavernosum to the end of the single penis.

Below the bladder there are two seminal vesicles and one prostate gland.

The scrotum and testes appear normal.

Taking the monster as a whole we find signs of doubling in its upper and lower ends, in the central nervous system, the respiratory system, the circulatory system, digestive system, bladder and urethra.

The central nervous system shows complete doubling of the brain and spinal cord.

The respiratory system is completely doubled.

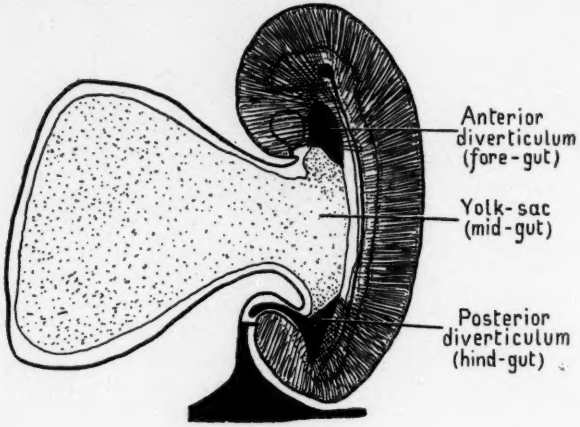


Fig. 7.

The circulatory system is doubled from above to the coeliac axis after which this system is single with the exception of certain branches distributed to the ani.

The spleen is single.

The bladder and urethra are partially doubled.

The digestive system is doubled completely as far as and including the lower part of the descending duodenum and also the liver and pancreas.

The ascending portion of the duodenum, the jejunum, illium, caecum and appendix are single.

The large intestine is doubled by means of a septum from its commencement at the caecum to the rectum after which separation into two is complete.

To explain the reason for the variation in doubling let us imagine an embryo in the early blastocyst stage (fig. 7) in which an attempt at twin formation occurs. Splitting takes place from the dorsal surface and extends to the head and tail ends, reaching the yolk sac but not implicating it. The

anterior and posterior diverticula of the archenteron being already formed will likewise be split.

With development, growth takes place more rapidly at the head than at the tail end and, as the diverticula grow at a similar rate, doubling will be much more complete in all structures developed from the anterior diverticulum, or fore gut, than in those formed from the posterior diverticulum, or hind gut.

The fission not having reached the yolk sac all structures developed from the mid gut will remain single. The structures developed from the fore gut are stated to be:

The pharynx.
Oesophagus.
Stomach.
Duodenum as far as and including the common bile duct.
The Liver and Pancreas.
Lungs and Heart.

All these structures are found doubled in the specimen and this agrees with the present knowledge of the development of organs from the fore gut and also with our suggestion that dorsal splitting of the embryo has taken place to the yolk sac only.

The structures developed from the posterior diverticulum of the archenteron or hind gut are stated by Keith to be:

The Colon from the splenic flexure to the anus.
The Cloaca, Bladder and Urachus.

The mid gut is said to form the rest of the alimentary canal from the duodenum to the splenic flexure of the colon.

In our specimen doubling commenced at the caecal end of the large intestine and was continuous from this point to the anus.

The fact that a continuous septum was found in the large intestine along its whole length and a similar condition in the bladder shows that fission occurred when the posterior diverticulum first made its appearance.

Growth of the tail end of the embryo caused lengthening of this diverticulum and the septum formed in this primary diverticulum was carried down with the lengthening tube.

The whole of the large intestine must therefore be formed from the same structure, that is from the hind gut, and the small intestine, including the ascending portion of the duodenum (and also the caecum), from the mid gut.

This explanation of the development of the gut, which appears to be correct, greatly simplifies the study of this subject, for it is shown that the essentially different parts of the alimentary canal such as small and large intestine are developed from mid and hind gut respectively.

Further the partial doubling of the bladder by a septum similar to the condition in the colon and the doubling of the pars prostatica and pars membranacea urethrae indicate that these structures are also developed from the primitive cloaca or hind gut.

In conclusion we consider it reasonable to assume:

(1) That splitting occurred in the early blastocyst stage when the anterior and posterior diverticula of the archenteron were forming.

(2) That both diverticula were affected by the splitting.

(3) That the yolk sac was not so affected.

(4) That the study of the double and single parts of the monster proves that all structures down to the lowermost part of the descending portion of the duodenum are developed from the fore gut, that all structures from this point to the commencement of the colon and including the caecum are developed from the mid gut, and that all structures below this point are developed from the hind gut.

We have to thank Professor Derry of the Department of Anatomy, School of Medicine, Cairo, for his kind help and criticism in the preparation of this paper.

A CASE OF CYCLOPIA

By SYDNEY SMITH, M.D., D.P.H.
Principal Medico-legal expert, Egyptian Government Service

AND BORIS BOULGAKOW, M.D.
Curator of Museums, Royal School of Medicine, Cairo

THE case of cyclopia which we are about to describe was observed in a 7½ months foetus, which was born alive but died immediately after birth. Pregnancy and delivery were quite normal but a certain degree of hydramnios was noticed shortly before delivery.

The foetus was well nourished with normally developed extremities and trunk. Its length was 32 cm. and weight about 1300 gm. (fig. 1).

The head was almost round, and was covered with hair which occupied about two-thirds of its surface. The hair commenced low down at the forehead just above the single eye.

The eye was situated in the middle of the front of the face. There was no nose. Below the position of the nose there was a structure which resembled a protruded tongue but which was proved to be the upper lip. Under the upper lip there was a small blind pit representing the mouth. The lower lip and chin were not present. The auricles of the ears were of large size and the lower poles were directed towards the middle line of the neck.

The rest of the body was normally developed.

THE ORBIT

Externally there was a single eye situated approximately in the middle of the face. Above the eye there was an eyebrow but the hair direction showed that this was composed of the outer halves of the right and left brows. The appearance of the outer canthi showed that they were the lateral canthi of the right and left eyes. In the middle of the lower margin there was a structure resembling the caruncula lacrimalis and on each side of this there was a triangular pigmented area. These structures indicate the fusion of two medial canthi. The photograph (fig. 1) shows this fusion of eyebrows and fusion of the medial canthi very clearly.

On dissection of the orbit one eyeball and one optic nerve were found. The eyeball was apparently single but on section its component parts were shown to have been produced by the fusion of two eyes. This was particularly well seen in the choroid and sclera.

The optic nerve on microscopical section was found to be single. The muscles of the orbit were disposed as follows:

Fig. 1.

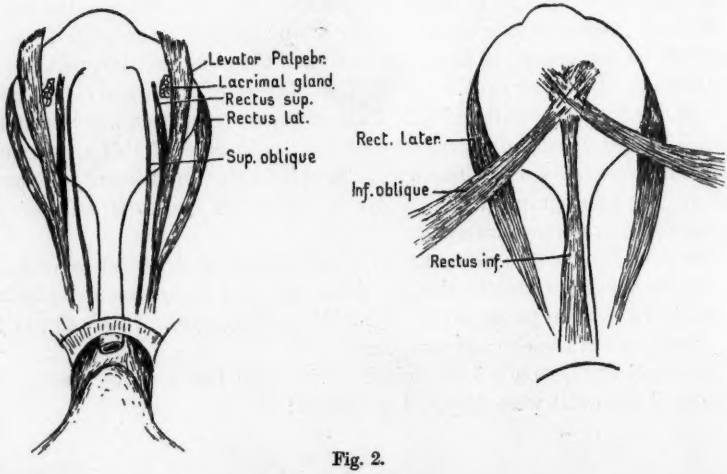

Levator Palpebr.
Lacrimal gland
Rectus sup.
Rectus lat.
Sup. oblique
Rect. Later.
Inf. oblique
Rectus inf.

Fig. 2.

From above two superior oblique muscles were seen close together near the middle line. On each side of these there was a superior rectus partially covered by the superior palpebral muscles which were situated somewhat laterally. On each side of the eye there was a lateral rectus muscle inclined towards the lower surface. From below, two inferior recti muscles were seen fused together in the middle line and from each side of the orbit an inferior oblique arose and passed towards the middle line, where it decussated with its fellow of the opposite side and was inserted with the fused inferior recti. On both sides of the eyeball there were lacrimal glands proved by microscopical examination. The disposition of the muscles proved that the cyclopian eye was formed by the fusion of a right and left eye (fig. 2).

THE SKULL

The skull was composed of normal occipital, parietal and temporal bones, but the two frontal bones were represented by a bone similar in size and appearance to the occipital bone and which proved to be the result of union of the two lateral portions of the frontal bones. There was no metopic suture and no fontanelles and the sutures between the bones were narrow (fig. 3). In the place of the fronto-nasal process and in the middle of the upper margin of the orbit a depression was observed. On each side of this depression a supraorbital notch was present. On removal of the vault, the orbital plates of the frontal bones were found to be fused in the middle line forming the roof of the orbit. The posterior part of this roof, however, was membranous in character and its posterior edge formed the upper boundary of a single optic foramen.

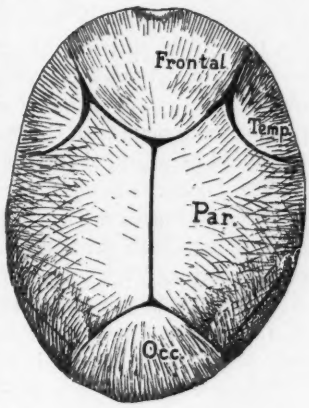


Fig. 3.

There was no sign of a crista galli, the cribriform plate of the ethmoidal bone, or of the pituitary fossa. The middle of the body of the sphenoid bone appeared to have been suppressed. The clinoid processes of the sphenoid were present and gave attachment to the tentorium cerebelli.

On examining the bones of the face the lower jaw was found to be absent and the maxillary bones were joined together in such a manner that the orbital surfaces of both were fused together to form the floor of the single orbit. Their frontal processes were situated below the orbit where they met in the middle line; the infraorbital foramina were situated on each side of these processes.

There were no nasal bones and no nasal cavity.

On the lower surface of the maxilla a cleft with a structure situated in it was observed between the palatine processes. This structure may represent

certain of the bones normally situated in the middle line which have been displaced downwards, such as the vomer and the ethmoidal bone.

There were no incisor teeth in the upper jaw; the central tooth appeared to be a canine followed by the 1st and 2nd molars.

As we mentioned in describing the bones of the skull the roof of the orbit was formed by the fusion of the orbital processes of the frontal bones and from the dura mater in its posterior part. The floor was formed by the fusion of the two maxillary bones and the lateral parts by the malar bones and great wings of the sphenoid.

DISSECTION OF THE NECK

The opening situated under the upper lip was 12 by 5 mm. in size and led into the mouth cavity. The latter, 18 mm. in depth, was lined with mucous membrane and had no communication with either the nasal cavity or the pharynx. When the skin and superficial tissues were dissected we found that the lower jaw was absent; the hyoid bone was found to be normal in appearance and situation. A rounded muscular mass, which might be regarded as the mylohyoid muscle, was attached to the middle of the body of this bone and other structures such as the stylohyoid ligament, stylohyoid and omohyoid muscles, etc., were normally situated and easily distinguished. The posterior part of the tongue with the epiglottis was situated on the posterior surface of the hyoid bone and the tongue was directed upwards.

The larynx was normally developed and all its cartilages were present. It was continuous with the trachea. The relationship to the pharynx was normal and both structures led into a common blind pharyngo-laryngeal cavity above. The mucosa of this cavity was continuous through greatly enlarged eustachian tubes with the mucous membrane of the middle ear. The tympanic cavity contained malleus, incus and stapes and was closed externally by the tympanic membrane, which was situated horizontally.

There was no thyroid gland present.

THE DURA MATER

The interior of the skull was lined with a thick membrane. There was no falx cerebri but the tentorium was developed apparently normally; its anterior border was concave and free, bounding a large oval opening. In front it was attached to the superior angle of the petrous part of the temporal bone on either side and in its continuation forwards was fixed to the anterior and posterior clinoid processes of the sphenoid bone.

The venous sinuses were situated normally, with the exception of the superior and inferior sagittal sinuses, which were not present.

THE BRAIN

The forebrain was horse-shoe shaped with the opening behind and the space between the limbs of the horse-shoe was roofed by pia and arachnoid. The two limbs passed backwards to the antero-lateral aspect of the cerebellum at the

level of the anterior corpora quadrigemina. On removal of the membranes the cerebral surface was found smooth, free from convolutions, and composed of two symmetrical halves. On the external aspect of each half there were two depressions in which were placed the anterior and middle cerebral arteries. The posterior cerebral artery was situated in the base of the brain and appeared on the surface between the back of the brain and the cerebellum (figs. 4 and 5).

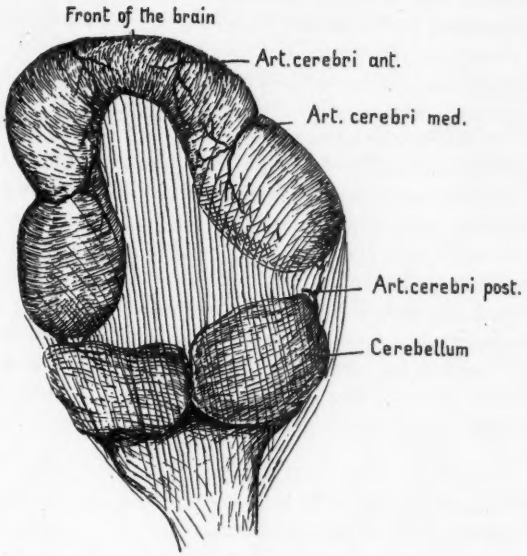


Fig. 4.

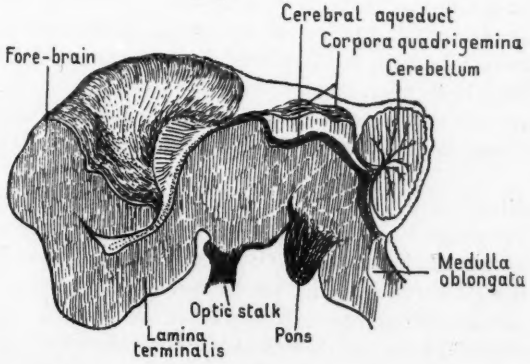


Fig. 5.

The brain appeared to be normal posterior to the corpora quadrigemina. The optic thalami were fused and on the upper surface there were structures resembling the taeniae directed towards the aqueductus cerebri. The commissures, fornix and corpus callosum were absent. The aqueduct continued forwards in the common central cavity, which communicated with the cavities in the forebrain through a large oval opening. On removing the pia mater from the internal and inferior surfaces of the brain, the choroidal plexus was withdrawn with it and a choroidal fissure was exposed on each side in a position corresponding to the lateral part of the great transverse fissure, but owing to the absence of the fornix and corpus callosum, the plexus was lying free above the corpora quadrigemina. From this position the plexus descended towards the foramen leading into the central part of the common lateral ventricles into which it was invaginated.

On the inferior surface of the brain, the part posterior to the pons appeared to be normal, but anteriorly there was no bilateral symmetry. In the place of the corpora mammilaria and tuber cinereum there was a raised area from the top of which a single optic nerve began. Anterior to the optic nerve no chiasma was found. The brain continued towards the anterior pole forming the lamina terminalis anterior. This lamina was thick and was continuous with the prosencephalon forming the lower wall of the central part of the lateral ventricle and at the same time took part in the formation of the oval foramen described above. The cerebral nerves were normal from the third onwards, the optic nerve was single and the olfactory tracts were absent.

SUMMARY

From the above dissection it is observed that the structures normally found in the middle part of the head and face are not present in the specimen. Thus there is an entire absence of the falx cerebri, the medial parts of the two frontal bones, the ethmoid, vomer, premaxilla, nose, philtrum of upper lip, anterior part of tongue, lower jaw, lower lip and thyroid gland.

In addition the mesial portions of both eyes are absent and the lateral halves have fused together to form an apparently single eye, and the bones which form the orbits have been reduced in a like manner with fusion of their lateral parts to form an apparently single orbit.

There is also complete absence of both olfactory lobes and nerves, absence of the mesial part of the base of the brain and the formation of a single optic nerve.

The brain itself shows, not a loss of its mesial parts, but a condition of suppressed development and it remains in the condition of the foetus in which the forebrain has just been developed and before the hemispheres have arisen. We have therefore in the production of a cyclopian monster, to assume that some abnormal process has taken place in the very early embryonic state by which the cells which would normally form the middle part of the face and anterior part of the head have been destroyed, and therefore

all these structures which should normally develop from these cells, including the fronto nasal process and mandibular arch, have not developed at all.

From the fact that the lateral portions of these structures are normally developed, namely, the lateral parts of the frontal bones, the maxillary processes of the mandibular arch, the malleus and incus from the posterior part of Meckel's cartilage, we are led to believe that there has been an actual destruction of the cells which should have formed the middle part of the frontal. pole of the embryo. The lateral parts have thereupon fused together in the middle line and have produced the apparently single eye of the cyclops and the other peculiarities noted.

This destructive process has penetrated to the forebrain, but whereas there has been an actual destruction of the central portions which should have formed the olfactory lobes, optic thalami, etc., the main effect on the prosencephalon appears to have resulted in a general stoppage of development.

THE HOMOLOGY OF THE ALA TEMPORALIS AND OF THE ALISPHENOID BONE

By H. LEIGHTON KESTEVEN, D.Sc., M.D., Ch.M.

Broom (1907 and 1911) recognises in the ala temporalis a remnant of the palatopterygoid cartilage, and in this homologisation he is followed by Watson (1916) and by Gregory and Noble (1924), the earlier contention of Gaupp (1902) that it is homologous with the basipterygoid of the lizard being deemed disproved by its origin independently of the processus alaris, which alone they considered to satisfy all Gaupp's arguments.

Whilst in accord with these observers in restricting Gaupp's homology to the processus alaris, I am not able to agree either with them or with Gaupp in the interpretation of the ala temporalis. I believe that it can be shown quite certainly to have been derived from the pila prootica, by an unbroken chain of modifications, without any such striking exchange of function on the part of primary elements as is postulated by the identification of Broom.

It may be emphasised before proceeding further that Broom's hypothesis involves the assumption that a primarily visceral element has by complete modification become converted into a cranial element, and this whilst other craniates quite closely related were able to enclose the brain with bones derived from the primordial cranium.

It is a noteworthy fact that, in their discussions of this problem, recent workers, excepting only Allis (1919), have failed to review the conditions in the Ophidia and the Aves, and yet a proper evaluation of the conditions in these is more helpful to a solution of the problem than perhaps all the other factors without those presented by these two types of chondrocrania.

Since Broom's homology arose from his observations of the development of the ala temporalis in *Trichosurus* (1909), it is peculiarly fitting that we accept the form and mode of development therein as typical for the higher vertebrates. As there is no question as to the homology of the processus alaris of the marsupials with that of the mammals, and the original independence of the ala temporalis has been recorded for several mammals, no objection can be taken to this procedure.

Broom's early stage of *Trichosurus* shows the two alae temporales lying free, lateral to a processus alaris represented by the outer margin of the carotid foramen (fig. 1). His later stage shows the two structures fused together, and the pterygoid bone developing on the under surface of the inner margin of the ala (fig. 2 A). For comparison with these I have reproduced in outline Broom's drawing of a stage of development of the chondrocranium of

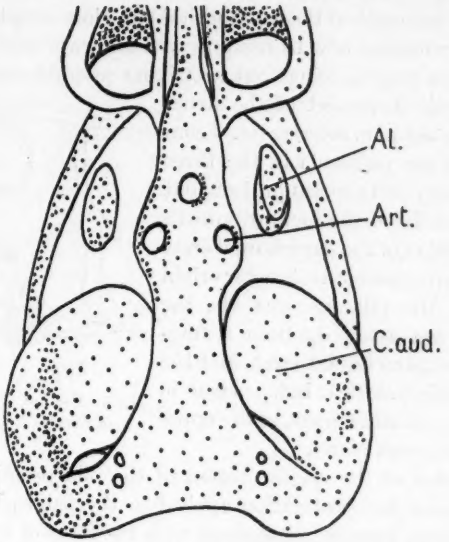


Fig. 1. Chondrocranium of *Trichosurus* showing the alae temporales before their attachment to the processus alaris (from Broom, 1909).

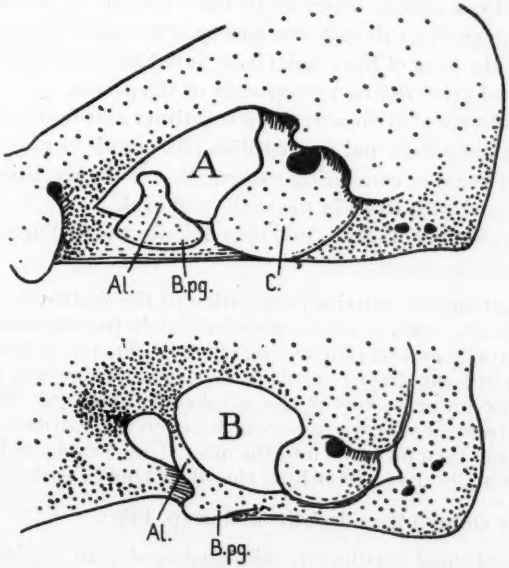


Fig. 2. A. *Trichosurus* at a later stage of development. B. *Dasyurus* of much the same age as A. Both these show the alae attached (from Broom, 1909).

Dasyurus similar to the last (fig. 2 B). In this form it will be seen that the lamina ascendens has reached the supraorbital bar, thus completing a veritable pila prootica. A reference now to Gaupp's well-known model of the chondrocranium of *Lacerta* (fig. 3) brings out a striking resemblance between these three chondrocrania in respect of the structures attached to the pars intermedia. From the under side of the trabecula in the three forms, the basipterygoid process projects out and down. In the lizard the forward growth of the prootic portion of the parachordal crest has given rise to an apparent trabecular origin for the root of the pila prootica. In the marsupial there has assuredly been a fragmentation of the parachordal crest, and the remnant of the pila prootica, independent in early stages, gains an attachment to the upper surface of the processus alaris.

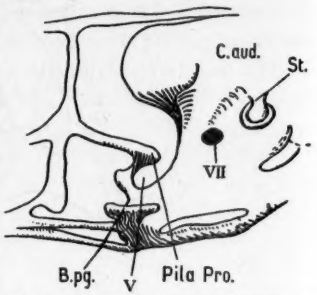


Fig. 3. Portion of the chondrocranium of *Lacerta* (from Gaupp, 1902).

This postulation of the fragmentation of the pila prootica is in no way more radical than a like postulation applied to the palatopterygoid arch by Broom, and appears more in consonance with the facts of later development than does Broom's interpretation, because this cartilaginous pellicle is situated above the level of the cranial base in the side wall of the primordial cranium and gives rise to a cranial bone; in all these features it resembles the pila prootica, and differs from the anterior moiety of the palatopterygoid, which is situated below the level of the cranial base, is not situated in the side wall of the cranium, and gives rise to a component of the palate.

Arranged thus the above observations constitute a strong case for regarding the therian ala temporalis and the reptilian pila prootica as homologous; but this contention receives convincing confirmation if the conditions in *Trichosurus* be compared with those in the snake and bird.

Parker and Bettany (1877, p. 193) thus describe the first appearance of the ala temporalis in the snake:

> Between the out-turned anterior termination of the basilar cartilage and the side wall of the otic mass is a large rounded notch, just opposite to the post-pituitary fontanelle and of similar size. Part of this notch is occupied by a small independent ear-shaped cartilage, having a narrow end forwards, and its edge convex inwards; this is the alisphenoid cartilage. The orbitonasal branch of the trigeminal nerve passes out between this cartilage and the auditory capsule, and then forwards into the orbit. The second and third divisions of the trigeminal also pass out behind this alisphenoid cartilage.

In an older embryo they describe it thus (p. 195):

> The small alisphenoid cartilage is still earshaped, and is placed somewhat longitudinally....A notch in the hinder part of the alisphenoid embraces the posterior division of the trigeminal nerve...and the remainder of the

trigeminal emerges from the cranial cavity in the space between the concave notch of the front aspect of the basilar plate and the concave edge of the alisphenoid.

The situation of this little ala temporalis is essentially the same as that of *Trichosurus* and its relation to the branches of the trigeminal nerve is the same, yet there can be no reasonable doubt that it is a veritable pila prootica.

We thus have within the reptilia, cartilaginous anlagen of the alisphenoid which present the same variability in their relations to the branches of the trigeminal nerve as the bones themselves do. I have already (1918) arranged the facts in this connection in an argument showing that this variability does not contra-indicate the homology of the variable structures, and with the justice of my conclusions Gregory and Noble (l.c.) are agreed, though they agree with Broom on the main question on other grounds.

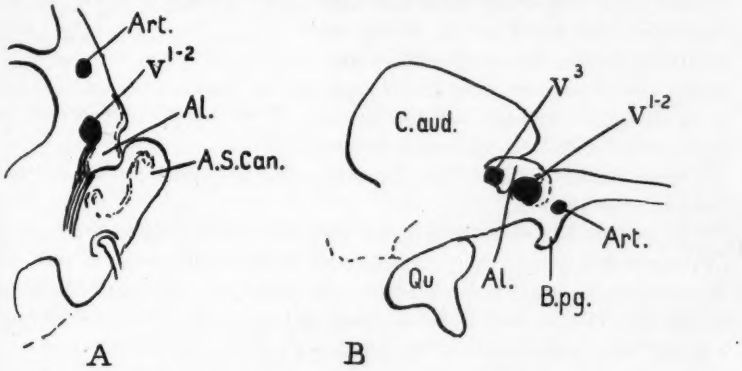


Fig 4. Portions of the chondrocranium of the snake (from W. K. Parker, 1879). A basal, B lateral views.

It must however be emphasised that the ala temporalis of the snake presents just those relations to the branches of the nerve on which much of the weight of Broom's homologisation of the epipterygoid rests.

If there be remaining any doubt as to the correctness of my identification of the ala temporalis in the snake I believe that it will be removed by a comparison of the snake chondrocranium with Howes and Swinnerton's well-known figures of the primordial cranium of *Sphenodon*, and the little less known drawing of that of *Tinnunculus* from Suschkin reproduced below (fig. 5).

Of the ala temporalis in the chondrocranium of the chick at the end of two weeks' incubation (a later stage of development than that illustrated of *Tinnunculus*) Parker and Bettany (l.c., p. 236) wrote:

The alisphenoid cartilage has become complicated in its relationships, being united with the fore part of the ear-mass above and below (the main part of the trigeminal nerve issuing between them); and also continuous by its base with the posterior clinoid wall and the side of the pituitary region.

Note that here again is a veritable pila prootica which presents the same relations to the branches of the trigeminal nerve that the epipterygoid presents. It is shown elsewhere in this communication that the portion other than the "main part of the trigeminal nerve" which does not issue behind the pila prootica is the first branch; this perforates the bone which is ossified from the pila and in all probability passes forward to the inner side of it.

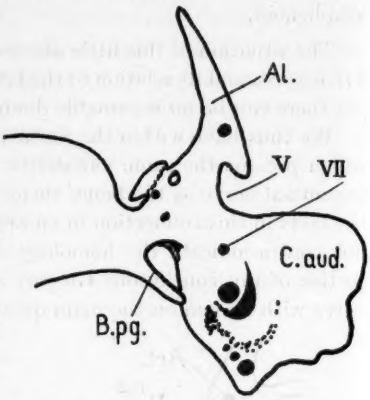


Fig. 5. Portion of the chondrocranium of *Tinnunculus* (after Suschkin from Kingsley, 1917).

Reviewing now the whole of the evidence adduced above, it must be conceded that a very strong circumstantial case has been made out in favour of regarding the ala temporalis of the mammals as derived from, and homologous with, the pila prootica of the lower vertebrates. If this be so then, of course, the bones which are developed from the pila are homologous with those developed from the ala.

Allis (1919) has recently reviewed these facts at greater length than is done in the preceding pages; unfortunately his conclusions therefrom are based on the relations to single nerve branches and roots, and are completely neglectful of all else. His review of the recorded facts is, however, a careful one, and, regarded as a compilation of the facts, is a very useful contribution.

The alisphenoid region of the adult skull.

It is a noteworthy fact that throughout the whole of the craniata the alisphenoid region of the cranium is enclosed with cartilage or bone, excepting only in the recent Lacertilia and Chelonia, some extinct reptiles and perhaps a few stegocephalians. It is also a fact that, excepting in the Theria and perhaps in some extinct reptiles, these alisphenoid cartilages and bones have been shown to be developed directly from the primordial cranium.

And it is not without significance that Broom's proposal in regard to the therian alisphenoid cartilages and bones has arisen from the study of certain bones in these extinct reptiles, and that the origin of these bones is the subject of speculation and beyond the reach of the elucidating evidence which embryology might be expected to throw on their origin.

Broom's homology rests on four "props":

1. "The very curious circumstance that almost invariably there is present either a columella-cranii or an alisphenoid, but never both" (Broom, 1907).
2. The relation of the alisphenoid to the branches of the trigeminal nerve.
3. The early independence of the ala temporalis in *Trichosurus*.

4. The form and situation and presumed relations to the branches of the same nerve of the so-called epipterygoid (Broom called it alisphenoid) in certain of the cynodont reptiles.

The statement in the first prop has been shown to be incorrect. I have elsewhere shown that the second prop is a quite unreliable support on which to rest questions of this kind (Kesteven 1918). We have seen in the last section of this communication that the early independence of the ala is not a reason for regarding it as a derivative of the palatopterygoid cartilage, and is no contra-indication to its being derived from the pila prootica.

It remains to examine the evidence adducible in constitution of the fourth prop; as a preliminary thereto the structure of the alisphenoid region of the cranium of the adult craniata will be briefly passed in review.

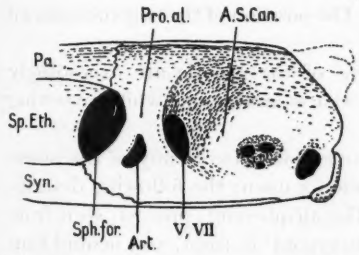


Fig. 6. The cranial wall of the adult *Hyla* see from within.

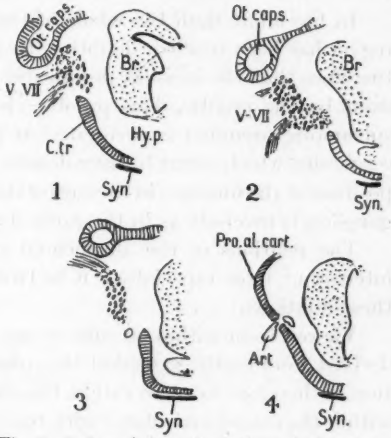


Fig. 7. 1, 2, and 3, sections through the chondrocranium of a *Hyla* tadpole in the region of the prootic foramen. 4, a section through the alisphenoid cartilage of the same specimen.

It needs not that the elasmobranchs be described in any detail; suffice it to remark on the completeness of the cartilaginous wall in the alisphenoidal region.

Though there are minor differences in the construction of the alisphenoidal region of the skull in the amphibia it seems justifiable to treat the conditions observed in *Hyla* as exemplary for the class; true, in some forms there is appreciably less ossification of the region than in the example selected. Such cases present a return to the elasmobranch condition, and by their very existence prove a community of inherited driving force in these divergent forms. This force is recognisable again as underlying and explaining the remarkable similarity of the adult cranium of *Polypterus* to the amphibian type, but anent

this more anon. In *Hyla aurea* I find that the alisphenoidal region is ossified by an extension of the prootic (figs. 6 and 7).

In early stages of development the trabecular crests extend up on each side to form complete side walls to the cranial cavity in this region, just as they do in *Rana*. The posterior boundary of the incisura prootica may fairly be regarded as the anterior limit of the prootic region. In front of, and a little lower than the incisura prootica there is another smaller perforation of the crista trabeculae; this transmits the arteria cerebralis. A little distance behind the incisura, the prominence of the anterior semicircular canal, bulging into the cranial cavity, gives rise to a recess between it and the incisura. The trigemino-facial ganglion lies against the cartilage in this recess, partly inside the cranial cavity but protruding through the incisura so that the greater portion of it lies outside the wall.

In the adult skull the whole of the crista trabeculae in the alisphenoidal region has been ossified, doubtless by extension from the prootic. It follows therefore that the incisura prootica is bounded behind, above, below, and in front by the prootic. This prootic "bridge" lying between the prootic and sphenoptic foramina is perforated at its base for the passage of the arteria cerebralis, which seems to have descended somewhat when compared with the position of the foramen in the earlier stage. The position of the trigemino-facial ganglion is precisely as in the early stage.

The relations of the alisphenoid process of the prootic are exceedingly interesting, more especially if it be treated as a separate bone while reviewing these relations.

Viewed from within no sutures are discoverable between any of the bones derived from cartilage behind the sphenoptic foramen; the following description is therefore to some extent fanciful. The alisphenoid (process) seen from within the cavity articulates with the synpterygoid[1] in front, and behind that is fused to the basisphenoid (region of the cranial floor). It forms the posterior border of the sphenoptic foramen and the anterior boundary of the prootic foramen; at the lower end of the latter it articulates with the lower antero-medial corner of the prootic, and with the same bone again above this foramen. This last articulation is continued up to the parietal and across the roof to the mid-line under that bone. The anterior limit of the alisphenoid (process) dorsally is immediately above the centre of the sphenoptic foramen.

As seen from without, the alisphenoid (process) articulates below in front with the synpterygoid and the lateral edge of the basisphenoid (region of the cranial floor); it appears to form the lower boundary of the prootic foramen, and behind this articulates with the prootic, extending a short distance back on the outer surface of that bone to reach the quadrate above the quadrate ramus of the synpterygoid. Dorsally the bone articulates with the parietal in front and the prootic behind.

[1] Believing that the pterygoids have been derived from the parasphenoid I have elsewhere proposed to designate that composite bone synpterygoid (Kesteven, 1916, 1919, 1925).

(Note. The appearance of extending on the quadrate is due to the presence of a groove (for a branch of the trigemino-facial nerve, issuing from the prootic foramen), which gives all the appearance of a separation between this bone and the prootic.)

As already stated, this description is to some extent fanciful; it however serves to accentuate relationships whose proper evaluation is essential to the correct interpretation of the various bones which come within the purview of the present discussion. Moreover this description gains in value if it be remembered that it is the natural description of the bone as it stands in the adult cranium. Without any knowledge of its ontogeny it would be described as above, in fact was so described by Owen, who moreover designated it alisphenoid (1848, p. 27, fig. 13).

If this bone be compared with the epipterygoid of *Capitosaurus* it will be found to present a remarkable similitude. Watson (1919) describes this bone as lying outside the original cranial wall, depending for that determination on the fact that the posterior end of the sphenethmoid, in front of it, lies closer to the middle line. Maybe this determination is correct, but equally it may be that the explanation is that there is in front of his epipterygoid a narrowing of the cranial cavity in conformity with olfactory lobes of smaller girth than the fore brain. If this explanation be correct, the resemblance between the "epipterygoid" of *Capitosaurus* and the alisphenoid process of *Hyla* is almost complete, the difference being that there is an hiatus above the incisura prootica where in *Hyla* the alisphenoid (process) meets the prootic bone.

The following description of *Capitosaurus* together with the drawing is taken from Watson (1919, pp. 27–8).

The Basisphenoid is represented by a paired ossification....Each bone lies on the dorsal surface of the parasphenoid, and is quite well ossified; it is perforated vertically....The outer corner of the bone touches the epipterygoid...the extreme lower lateral border touching the pterygoid.

The epipterygoid...lies in the angle between the quadrate ramus and the horizontal part of the pterygoid. It has an otic process reaching up in close contact and, in some regions in sutural connection with the inner end of the quadrate ramus of the pterygoid to the pro-otic. The inner part of the dorsal end of the otic process reaches up to the skull roof, or very nearly so; laterally it is depressed to form with the prootic and pterygoid the lower border of the foramen of the vena capitis dorsalis...the otic process gives origin to the main mass of the bone, which runs forwards and inwards and upwards as a processus ascendens, separated by a deep narrow notch, widening into a foramen, from the otic process.

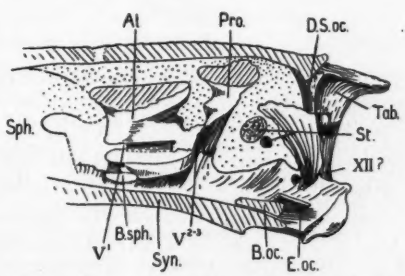


Fig. 8. Interior view of the side cranial wall of *Capitosaurus* (from D. M. S. Watson, 1919).

On the endocranial surface the ascending process forms a large area lying outside the original cranial wall (whose position is indicated by the posterior end of the sphenethmoid). The bone articulates with, may in fact be fused to, the anterolateral corner of the basisphenoid....

It will be observed that throughout this description Watson has designated "epipterygoid" that which I would term alisphenoid.

The ganoids present three distinct types of cranium, the elasmobranch is represented by the accipenserids, the amphibian by the Crossopterygii and the teleostean type by the Holostei.

Allis (1922) states that in *Polypterus* the hinder end of each vertical lamina of the "sphenoid is everywhere in contact with the cartilage (of the prootic

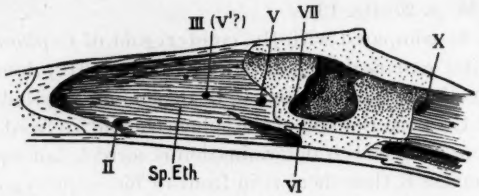


Fig. 9. Interior view of the side cranial wall of *Polypterus* (from Allis, 1922).

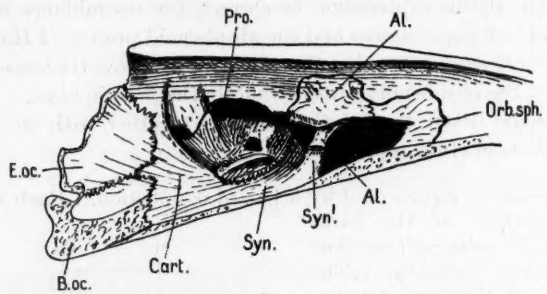


Fig. 10. Interior view of the side cranial wall of *Amia*.

region) excepting at its ventro-posterior corner where it articulates with the anterior edge of the mesial plate of the ascending process of the parasphenoid" (synpterygoid). He further describes the incisura prootica as being cut out of this hinder end (fig. 9).

In *Amia* the alisphenoid is everywhere in contact behind with the cartilage of the prootic region except its ventro-posterior extremity, which is in contact with the mesial plate of the ascending process of the synpterygoid. Quite similarly to the hinder end of the "sphenoid" of *Polypterus*, it is situated so as to have the incisura prootica on its posterior border. In the basisphenoid region the skull floor is covered by cartilage. This cartilage is continued out and up the inner face of the ascending process of the synpterygoid to the alisphenoid. In a skull which is completely devoid of cartilage, the articulation of alisphenoid and basisphenoid cartilage is quite clearly indicated by

the abrupt outstanding lower end of the alisphenoid to the inner side of the articulation with the synpterygoid (fig. 10).

If now the alisphenoidal regions of *Hyla*, *Polypterus*, and *Amia* be compared, it is contended that there should be no doubt that the osseous structures are completely homologous. This may at first sight appear to be stretching the idea of homology unduly, since one is developed from the prootic centres of ossification, the second is developed in continuity with the orbitosphenoid, and the third independently of both those structures. On the other hand, all three are developed in the same region of the skull, in the same relation to the trigeminal nerve, and, finally, from the primordial cranial cartilage.

The inference to be drawn from the observed facts is as follows.

From a common ancestor these animals have received a chondrocranium more or less complete in respect of the side walls; on this has been grafted, also by hereditary force, a tendency to ossification of those walls. The three forms under review seem to indicate that in the earlier stages of the process of ossification there was no settled plan in the fragmentation of the ossified walls, but that ossification, having commenced in certain regions, extended into the contiguous areas of cartilage. The explanation of the plan of fragmentation ultimately adopted is apparently recoverable from a consideration of the fenestration of the side wall. The suture between alisphenoid and orbitosphenoid continues the sphenoptic fissure upwards, and similarly the suture between alisphenoid and prootic is situated directly above the trigeminal foramen. In a similar manner the suture between the exoccipital and opisthotic is above the foramen for the vago-accessorius nerve, and the sutures between the periotic bones radiate from the internal auditory meatus. It is conceivable that these fenestrae, by imposing isthmian barriers to the even and rapid spread of ossification, determined the development of centres of ossification on either side thereof.

If this be so we may designate such bones as those of *Hyla* and *Polypterus* "predeterminate" alisphenoids as distinct from the "determinate" alisphenoids of more advanced types, recognising at the same time that they are essentially homologous bones.

Among the Teleostei the alisphenoid is always well developed, and arises as an ossification of the cartilage of the side wall of the cranium in front of the ear capsule. Inferiorly the bone articulates with the basisphenoid and with the synpterygoid; in front of this articulation it bounds the sphenoptic fissure superiorly, and may or may not articulate with the orbitosphenoid in front of that fissure. Superiorly the alisphenoid articulates with the frontal and posteriorly with the prootic and sphenotic. In some cases, e.g. *Epinephelus* (fig. 11) the bone takes no share in the boundary of the incisura prootica, in other forms, e.g. *Tandanus* (fig. 12), it forms the anterior and part of the superior boundary of the incisura. Apparently the condition observed in *Epinephelus* is uncommon and without significance, I find that in closely related genera the bone shares in the bounding of the prootic foramen much as in *Tandanus*. In

those fishes in which an eye muscle canal is developed, that canal separates the articulation between the basisphenoid and synpterygoid; in other fishes in which the canal is not present these two articulations are in contact.

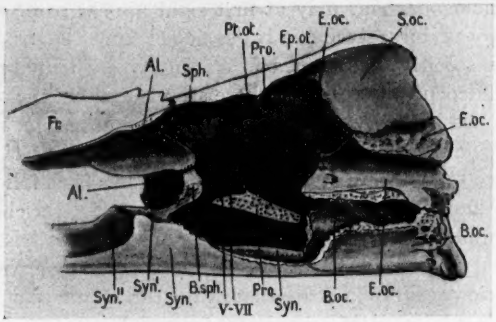


Fig. 11. Interior view of the side cranial wall of *Epinephelus*.

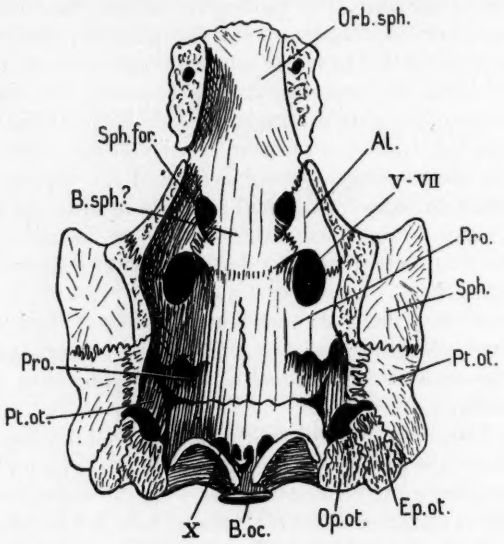


Fig. 12. The floor and side walls of the cranium of *Tandanus*.

The alisphenoid of *Crocodilus johnsoni* is the only bony component of the side wall of the cranial cavity in front of the periotic bones. It is articulated to the basisphenoid at the side of the pituitary fossa, and, behind this, with the anterior inferior process of the prootic, which forms the lower boundary of the gasserian fossa. The alisphenoid forms the anterior boundary of the fossa and meets the prootic bone again above it. Along the roof, the alisphenoid articu-

lates with the parietal and frontal bones. The sphenoptic foramen is bordered laterally by this bone and medially by the rostrum basisphenoidei; forward of the rostrum the gap between the two medial free margins of the alisphenoids is closed by the sphenoidal membrane.

Viewed from the outside, most of these relations can be made out. In addition a suture with the quadrate above the gasserian fossa is seen, and the suture with the prootic is hidden by that bone except above and below the fossa (fig. 13).

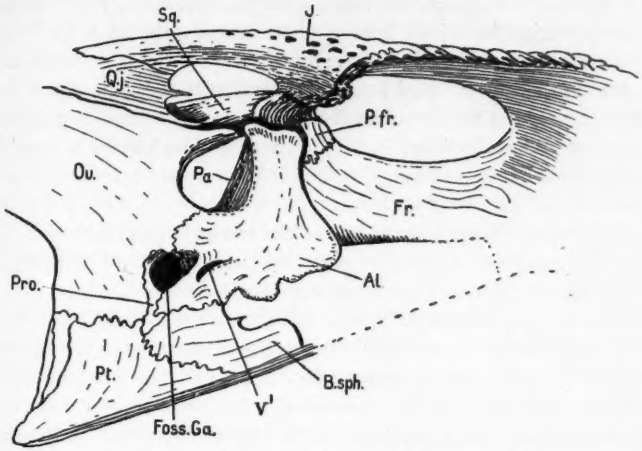


Fig. 13. The alisphenoid region of the skull of *Crocodilus johnsoni*.

It has already been stated that the gasserian fossa is bounded in front by the alisphenoid and below by the anterior inferior process of the prootic; its posterior and upper boundaries are also supplied by this latter bone. Not only do these two bones form the boundaries of the inner aperture of the fossa but they also form the walls of the fossa itself. On the outer side, however, the quadrate forms half of the upper and all of the posterior margin of the fossa. The front wall of the fossa, i.e. the alisphenoid bone, is perforated near the outer margin for the passage forward of the first branch of the fifth nerve.

The alisphenoid bone is produced laterally above to meet the postfrontal on the outer side of the supratemporal fossa, and in this situation it almost meets the anterior superior process of the quadrate.

It will be observed that, though the alisphenoid bone extends down below the external aperture of the gasserian fossa (incisura prootica), it does not reach the quadrate ramus of the pterygoid; a slip of the prootic bone intervenes. This slip of bone differs from the rest of the prootic. When the floor bones of the cranium are disarticulated from the side wall (as may be readily done in a young specimen) the lower articulating edge of the prootic is brought into view. The slip of bone in question can now be seen to project well below the

"processus inferior"; that process and the main body of the bone articulate with the basisphenoid by synchondrosis, whilst this superficial downwardly projecting lamina articulates by true suture with the same bone and with the pterygoid behind.

Crocodilus presents us with a distinct transition stage in the adult cranium. So far as we have gone all the alisphenoid bones are situated in front of and medial to the three branches of the trigeminal nerve. This holds good also for the crocodiles in very young specimens, but very soon after hatching the first branch of the nerve becomes covered on the outside for a short distance in front of the gasserian fossa by a lamina of the alisphenoid bone. To this extent then it can no longer be stated that the first branch of the fifth nerve is lateral to the bone. It should be noted in this connection that the ganglion does not lie on the outer side of the bone (as it lies outside the sphenoid membrane in the lacertilians and chelonians) in the adult crocodile, but in a fossa formed between the alisphenoid and prootic. It has been pointed out both by Shiino (1914) and myself (1918) that this alisphenoid is developed from the pila prootica in front of all three branches of the nerve. Nevertheless it is a fact that, were the ganglion fossa widened at its inner end, then in the adult we should have all the appearances present in the snake.

In the snake the alisphenoid bone is intimately fused with the prootic exactly as in *Hyla*, and it presents all the essential relations to the surrounding bones that have been detailed in the description of *Crocodilus*. The gasserian fossa is formed between the alisphenoid and the prootic as in the crocodile. The internal orifice of the fossa is distinctly larger than either of the external. Be it noted that the external orifice is distinctly double, the first branch of the fifth nerve issuing from the anterior, and the other two branches through the posterior external foramen.

Attention has already been drawn (*antea*, p. 3) to the fact that this alisphenoid bone is developed from a pila prootica which separates the first branch of the fifth nerve from the second and third, exactly as the bridge of bone between the two external foramina of the gasserian fossa separates them.

In the bird skull the fossa is found opened right out on the inner aspect of the alisphenoid bone.

The alisphenoid of *Dromaeus* is in no way peculiar; it has been selected here because the large basipterygoid processes and their relation to the pterygoids present a greater resemblance to the reptilian condition than is the case in the majority of birds.

The bone articulates with the basisphenoid on either side of the pituitary fossa, and lateral to that with the prootic; the line of suture with the prootic crosses the cranial floor and climbs the side wall for a little distance till the parietal is met. The line of suture with the parietal bone turns forward along the side wall to meet the sphenoidal lamina of the frontal bone; this suture crosses the front wall of the cavity till the small orbitosphenoid is met above and to one side of the optic foramen. A short suture between the alisphenoid

and the orbitosphenoid brings us to the upper margin of the optic foramen quite close to the middle line. Following the lateral margin of the optic foramen downward brings us to the anterior end of the suture with the basisphenoid.

The foramen rotundum lies just at the lateral end of the suture with the basisphenoid. Though it appears to interrupt this suture it really perforates the alisphenoid bone and the *external* orifice is situated well above the line of suture. The foramen ovale interrupts the suture between alisphenoid and prootic just behind and to the outer side of the foramen rotundum. To the inner side of the two foramina there is a fossa which lodges the gasserian ganglion (gasserian fossa).

It is noted, *en passant*, that the prootic and parietal meet, and that the squamosal is thereby excluded from sharing in the constitution of the inner wall of the cranial cavity.

Most of the sutures above described can also be seen from the outside. The squamosal bone covers the ascending portion of the suture with the prootic; the rest of that suture is visible on the roof of the tympanic cavity to the inner side of the otic ramus of the quadrate. That ramus must be removed before the inner end of the suture between the alisphenoid and anterior edge of the squamosal can be brought into view; it lies immediately to the inner side of the quadrate process of the squamosal. Seen from outside, the suture with the basisphenoid extends horizontally outwards to the inner end of the suture with the squamosal, the basisphenoid itself bulging forward below it. The basipterygoid process of the basisphenoid stands out, down, and forward from the antero-ventral face of this prominent anterior mass of the bone.

It is almost superfluous to point out that in *all* its relations this bone resembles that of the Mammalia. On the other hand it resembles just as completely the alisphenoid of the snake in all its relations to the bones of the cranial cavity and to the brain and nerves, excepting only that in the snake the gasserian fossa lies between the hinder end of the bone and the fore end of the prootic just outside the cranial cavity, instead of being a depression on the floor thereof; a difference so slight that it would be abolished if the inner aperture of the fossa were opened out a little further.

One naturally turns to Broom or Watson for details of the skull in the cynodonts; the following descriptions and figures are therefore taken from Broom (1911, p. 905):

> The alisphenoid bone . . . is well seen . . . in the Cape Town specimen of *Cynognathus berryi* (fig. 14). The upper portion of the bone is irregularly quadrilateral. The upper side articulates with the parietal, and the posterior with what I believe to be the prootic. Between the prootic and the alisphenoid are two large oval foramina. At the posterior and lower corner the alisphenoid is continued as a slender bone to the quadrate. At its anterior and lower corner it meets the pterygoids and clasps the basisphenoid. There appears to be an opening into the brain cavity between the base of the alisphenoid and the basisphenoid.

(p. 908)

Diademodon resembles *Gomphognathus*. . . so closely that there is some reason for suspecting that *Diademodon* may be immature *Gomphognathus*. . . . The alisphenoid in all its relations is very similar to that of *Cynognathus*. At its lower end near where it meets the pterygoid is an opening into the brain cavity, and most probably it was by this opening that the carotid artery entered the cranium (fig. 15).

Omitting the prototherians, in which the form and relations of the bone have recently been fairly exhaustively reviewed by Watson (1916), myself

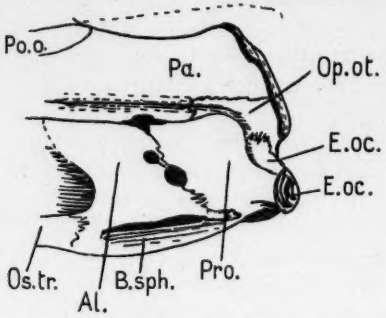


Fig. 14. The alisphenoidal region of the skull of *Cynognathus berryi* (from Broom, 1911).

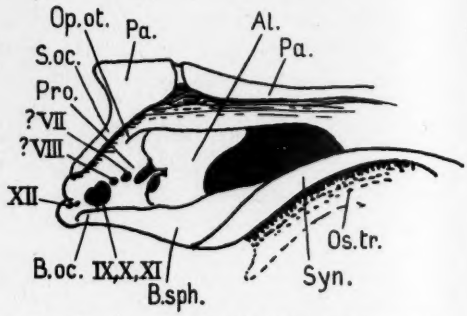


Fig. 15. Interior view of the side wall of the cranium of *Diademodon* (from Broom, 1911).

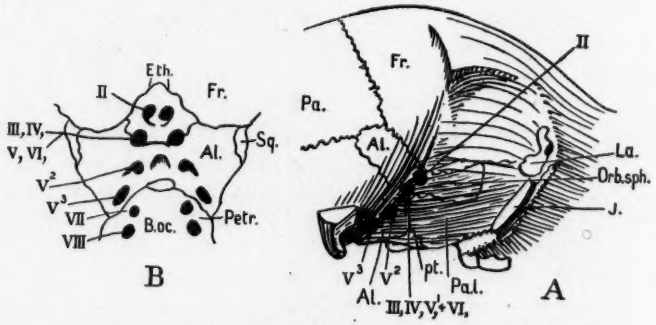


Fig. 16. A. Side wall of the skull of the dog, the zygomatic arch cut away to show the extent of the alisphenoid and the various foramina. B. The same from above.

(1918), and Gregory and Noble (1924), the mammalian alisphenoid presents a few variations calling for comment in the present connection.

The relation to the branches of the fifth nerve is not constant even in the higher mammals. The three branches may issue through separate foramina, as in the dog (fig. 16), in which case the first branch only is medial to the bone. In other forms the second as well as the first branch lies internal to

the bone, the foramen rotundum being merged with the sphenoidal fissure; this is the case in the sheep (figs. 17 and 18).

It is important to note that these differences are predetermined in the chondrocranium. Esdaile (1916), after describing the fenestration of the ala

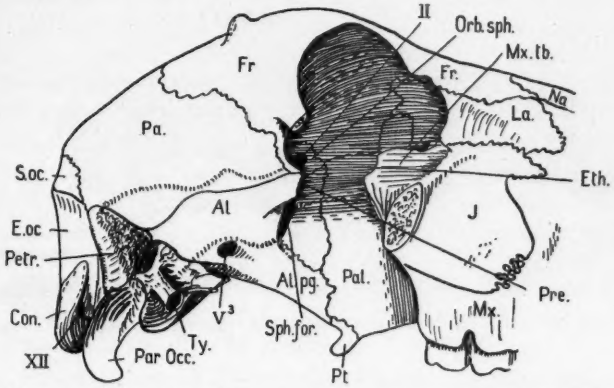


Fig. 17. Side view of sheep's skull. The squamosal bone has been removed, and the jugal and the post-orbital process of the frontal cut short to expose the alisphenoid bone and the disposition of the bones in the temporal fossa.

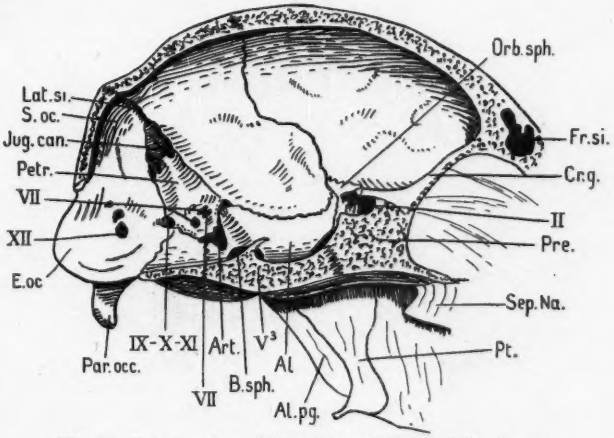


Fig. 18. Interior view of the side cranial wall of the sheep.

temporalis of *Perameles* by the foramen rotundum, says that it is interesting to note that in *Sus*, as observed by Mead, the ala temporalis is not perforated by the maxillary nerve, which passes out of the cranium, together with the second, third, and fourth cranial nerves, and the first division of the fifth, by the foramen lacerum anterius.

None of the higher mammals possess that backward extension replacing

the quadrate wing of the pterygoid which has been emphasised as characteristic of the epipterygoid (alisphenoid) of the cynodonts. This process is, however,

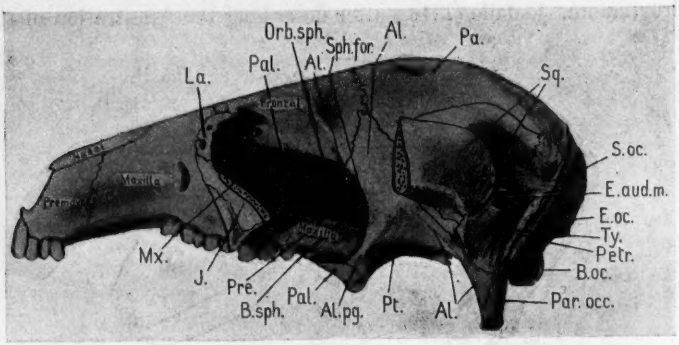


Fig. 19. Side view of the skull of *Macropus*, the zygomatic arch removed.

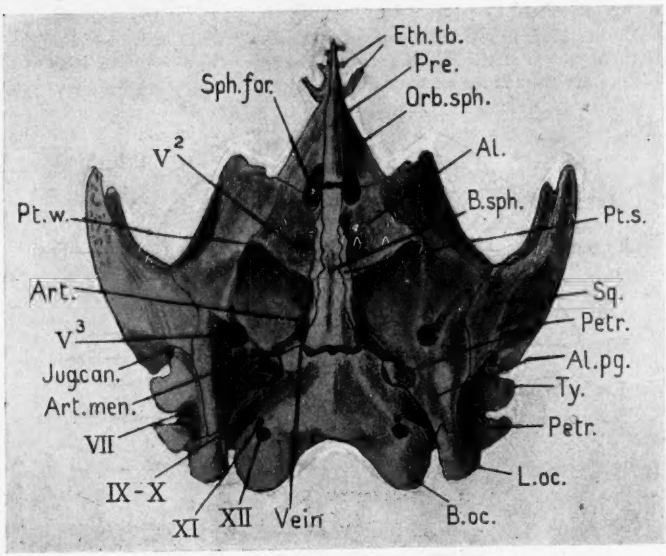


Fig. 20. *Macropus*. The pterygoid bone and the whole of the bones in front of the alisphenoid and below the orbitosphenoid have been removed to expose the alisphenoid and the foramina.

preserved in certain of the primitive anteaters, and is particularly well developed in some of the marsupials, and in none is it shown better than in the genus *Macropus*. In this form it extends well down the paroccipital process of the exoccipital bone (fig. 19). Except for the "postpterygoid process" the

extent and relations of the alisphenoid shown in the drawing of the base of a partially disarticulated skull of *Macropus* (fig. 20) is fairly exemplary of the conditions throughout the Mammalia.

Broadly reviewing the foregoing descriptions of the alisphenoid bone, it may be stated that in every case this bone articulates with the basisphenoid and pterygoid or synpterygoid between the incisura prootica and the sphenoidal fissure, that it articulates with the prootic element of the otocrane above the incisura prootica and with the orbitosphenoid above the sphenoidal fissure when that bone is present, and with the parietal and frontal bones along its upper edge.

In every case in which its development has been studied it has been shown to develop from cartilage which is either continuous with that of the rest of the chondrocranium from its first appearance, or very early becomes continuous therewith.

In the lower craniates it has been shown that this bone is ossified indifferently from centres of ossification either in front of or behind it. In the higher forms it is seen to ossify from its own specific centre.

It has been suggested that this independent centre of ossification, in common with all the other centres of ossification, is the direct result of the fenestration of the cranial wall.

Since this fenestration was doubtless present in the side wall of the hypothetical procraniate and was demonstrably handed down to all its descendants, this suggestion explains why the centres of ossification are found in essentially the same places in the crania of both the teleosts and the reptiles, although it seems highly improbable that these animals had a common ancestor in whose cranial walls the pattern of fragmentation of the ossification had been determined. In other words the suggestion supplies a mechanical explanation, and does not force us to requisition an inherited potential pattern to explain the observed facts.

So much for the similarities; it may be justly said of them that they appear to be fundamental and primary in origin and character.

What of the dissimilarities? These all centre round the relation to the branches of the fifth nerve, for even the independence of the ala temporalis in the mammals becomes significant only when its relation to the branches of this nerve are considered.

In the Amphibia, teleosts, and crocodile all three branches of the nerve are lateral to the bone. In the snake, birds, cynodonts and some mammals the first branch of the nerve is medial to the bone, whilst in most mammals the first and second branches are medial to the bone. Broom himself remarked (1911, p. 922), "In the mammal the alisphenoid differs from that of the cynodonts mainly in having the second and third branches of nerve V passing through it instead of behind it." Yet whilst maintaining the homology of the alisphenoids in the cynodonts and mammals he denies the homology of those of cynodonts and lower forms partly because the first branch of the nerve

passes behind the bone in these lower forms. I have not been able to find any explanation of this apparent inconsistency either in the structures concerned or in the literature.

It is incontrovertible that the relation to the branches of the nerve is variable, not only as between the lower vertebrata and the mammals but also as between the cynodont and mammals and within the Mammalia as well.

It may be said of these dissimilarities that they do *not* appear to be either fundamental or primary in origin and character.

It is admitted that Gregory and Noble have made out a convincing case in favour of regarding the "epipterygoid" of such forms as *Diademodon* and *Cynognathus* as homologous with the alisphenoids of the mammals; on the other hand they have not proved that these "epipterygoids" are homologous with those of other reptiles. Broom's drawing of *Bauria* reproduced on p. 442 proves nothing in favour of such a contention. It depicts a typical epipterygoid attached below to the pterygoid bone, and a true alisphenoid in exactly the position of the "epipterygoid" of *Diademodon* as depicted on p. 449, fig. 8 B.

I would (with no little trepidation, remembering whose conclusions I am criticising) suggest that the palaeontologists are allowing themselves to be led astray by adult similarities which are purely secondary. I am emboldened to suggest this by the remembrance that both Broom and Gregory (than whom we have no more keen and capable observers) made the mistake of homologising the alisphenoid of the crocodile with the epipterygoid of other reptiles on just such evidence as is available in the present connection.

Finally, reviewing the whole of the facts, we may conclude that the alisphenoid bones are homologous throughout the whole craniate series.

Bullahdelah
New South Wales
June 1925

LITERATURE

Allis, E. P. (1919). "The homologies of the alisphenoids of the *Sauropsida*." *Journ. Anat*, LIII.
—— (1922). "The Cranial Anatomy of *Polypterus*." *Ibid.* LVI.
Broom, R. (1907). "On the Homology of the Mammalian Alisphenoid Bone." *Rep. S. African Assn. Adv. Sci.*, pp. 114–115.
—— (1909). "Observations on the development of the Marsupial Skull." *Proc. Linn. Soc. New South Wales*, XXXIV.
—— (1911). "On the Structure of the Skull in the Cynodonts." *Proc. Zool. Soc. Lond.*, pp. 893–925.
Esdaile, P. C. (1916). "On the Structure and Development of the Skull and Laryngeal Cartilages in *Perameles*." *Phil. Trans. Roy. Soc. Lond.*, CCVII.
Gaupp, E. (1902). "Über die Ala Temporalis des Säugerschädels, etc." *Anat. Heft.* (Merkel u. Bonnet), Heft 61, 19 Bd., Heft 1.
Gregory, W. K. and Noble, G. K. (1924). "The Origin of the mammalian Alisphenoid Bone." *Journ. Morph. and Physiol.*, XXXIX.
Kesteven, H. Leighton (1916). "The Relation of the Amphibian Parasphenoids." *Journ. Anat. and Physiol.*, L.
—— (1918). "The Homology of the Mammalian Alisphenoid and of the Echidna-pterygoid." *Journ. Anat.*, LII.
—— (1919). "The Pterygoids in Amphibia and Reptiles and the Parasphenoid." *Journ. Anat.*, LIII.

KESTEVEN, H. LEIGHTON (1925). "Contributions to the Cranial Osteology of the Fishes, No. 1." *Records Austr. Mus.*, XIV.

—— (1925). "A third contribution to the Homologies of the Parasphenoid, Ectopterygoid bones and of the Metapterygoid." *Journ. and Proc. Roy. Soc. New South Wales*, LIX.

KINGSLEY, J. S. (1917?). "Outlines of Comparative Anatomy of Vertebrates." London, John Murray.

OWEN, RICHARD (1848). "On the Homologies of the Vertebrate Skeleton." London, R. and J. E. Taylor.

PARKER, W. K. (1879). "The Structure and Development of the Skull in the Common Snake." *Phil. Trans. Roy. Soc. London.*

PARKER, W. K. and BETTANY, G. T. (1877). "The Morphology of the Skull." London, Macmillan and Co.

SHIINO, K. (1914). "Studien zur Kenntniss des Wirbeltierskopfes. I." *Anat. Heft.*, Bd. L.

WATSON, D. M. S. (1916). "The Monotreme Skull." *Phil. Trans. Roy. Soc. London*, CCVII B.

—— (1919–20) 'The Structure, Evolution and Origin of the Amphibia." *Phil. Trans. Roy. Soc. London*, CCIX B.

INDEX OF ABBREVIATIONS USED ON THE ILLUSTRATIONS

Al.	alisphenoid bone or ala temporalis.
Al.pg.	pterygoid wing of the alisphenoid bone.
Art.	carotid artery or its foramen.
Art.men.	meningeal artery.
A.S.Can.	anterior semicircular canal.
B.Oc.	basioccipital bone.
B.Pg.	basipterygoid process.
Br.	the brain.
B.Sph.	basisphenoid bone.
Cart.	cartilage.
C.Aud	auditory capsule.
Con.	condyle.
Cr.G.	crista galli.
C.Tr.	trabecular crest.
D.S.Oc.	dermosupraoccipital.
E.d.si.	extra-dural sinus.
E.Oc.	exoccipital.
Ep.ot.	epiotic.
Eth.	ethmoid.
Eth.tb.	ethmo-turbinals.
Ex.Au.M.	external auditory meatus.
Fl.Foss.	floccular fossa.
Foss.Ga.	gasserian fossa.
Fr.	frontal.
Fr.Si.	frontal sinus.
Gl.	glenoid surface.
Hyp.	hypophysis cerebri.
J.	jugal bone.
Jug.Can.	jugular canal.
La.	lacrymal bone.
Lat.S.	lateral sinus.
Mx.	maxilla.
Mx.Tb.	maxillo-turbinals.
Na.	nasal bone.
Ob.	orbitosphenoid bone.
Op.Ot.	opisthotic bone.
Opt.Fr.	optic foramen.
Orb.Sph.	orbitosphenoid bone.
Os.Tr.	transverse bone.
Ot.Caps.	otic capsule.
Pa.	parietal bone.
Pal.	palatine bone.
Par.Occ.	paroccipital process.
Petr.	petrosal bone.
Pila Pro.	pila prootica.
Po.O.	post orbital bone.
Pre.	presphenoid bone.
Pro.	prootic bone.
Pro.Al.	alisphenoid process of the prootic bone.
Pro.Al. cart.	cartilage which subsequently ossifies as the alisphenoid process of the prootic bone.
Pt.	pterygoid bone.
Pt.S.	articular surface for body of pterygoid bone.
Pt.W.	articular surface for wing of pterygoid bone.
Pt.Ot.	pterotic bone.
Q.J.	quadrato-jugal bone.
Qu.	quadrate bone.
Sel.	sella turcica.
S.Oc.	supraoccipital bone.
Sp.Eth.	sphenethmoid bone.
Sph.	sphenotic bone.
Sph.for.	sphenoptic foramen and sphenoid fissure.
Sq.	squamosal bone.
St.	stapes.
Syn.	synpterygoid.
Syn′.	ascending process of the pterygoid bone.
Syn″.	medial (vomerine) plate of the pterygoid bone.
Tab.	tabular bone.
Ty.	tympanic bone.
Vein.	a vein from the cavernous sinus.

II, III, IV, V, V^1 V^2, V^3, VI, VII, VIII, IX, X, XI, XII. These symbols are used to indicate the foramina through which the corresponding nerves issue.

THE DISAPPEARANCE OF THE PRECERVICAL SINUS

By J. ERNEST FRAZER, F.R.C.S.
Professor of Anatomy in the University of London

THERE is much vagueness about the accounts given of the precervical sinus in the human embryo. In most cases the works dealing with the subject record its existence and satisfy themselves with the general assertion that it closes early and disappears. The general belief seems to be that there is fusion between the second external arch and the hinder and lower border of the sinus, so that this is rapidly reduced to an ectodermally lined cyst, opening on the surface by a drawn-out duct, and having the third and fourth arches and external grooves in its floor, with the second "external pharyngeal duct" opening into the neck of the cyst: this idea is apparently founded on Rabl's work on the mole, but the books of reference do not say much about the matter. This conception fits in with the current notions about "branchial remnants" in the neck, and the present writer, among others, was content to take it as practically correct, for it seemed to agree well enough with what was noticed incidentally when working on questions connected with the development of the pharynx and its derivatives. Recently, however, he has had reason to go into the matter directly, and the unexpected results obtained in this investigation seem worthy of consideration in full. It was found, as will be shown in this paper, that the sinus does not close at all in the sense usually understood, that the very small external fourth arch is covered in, but the third arch remains on the surface of the neck, and that no fusion normally occurs between the second arch (except perhaps at its upper part) and the structures behind it. Failure of these results to meet the seeming needs of the clinical pathologist, although regrettable, do not constitute any valid argument against them, derived as they are from careful study of normal embryos in good condition; nevertheless, some consideration of the abnormal conditions that are not so rarely found in the neck is certainly desirable, and a few words about some points on this side of the question are contained in a short addendum to the paper.

The *precervical sinus*, a result of the disproportionate size and growth of the outer pharyngeal arches, begins to show on the surface at an early stage. Fig. 1 (Pl. I), the head of an embryo of less than 5 mm. in total length, gives a very good idea of this early appearance of the sinus, and of its boundaries. The third and fourth arches are visible in a triangular area, slightly depressed, in front of which the second arch is prominent and its groove very evident. Above and behind is a clearly defined broad area, especially well marked

behind. The pericardium is below the sinus, but does not form its lower boundary directly: this is made by a clearly seen *epipericardial ridge*, which is continuous behind with the caudal boundary, and disappears from view, in front, below the lowest visible part of the third arch. The upper, hinder, and lower boundaries are thus continuous with each other round the field of the sinus, and require more particular examination.

A definite groove or depression separates the upper and hinder boundaries from the sinus field, and it is to be noted that the upper part of the second arch is clear, and is not continuous with the upper boundary: the upper end of the second groove comes in between them. This limiting region belongs to the area of paraxial mesoderm. It is continuous above with the bed of paraxial mesoderm in which the otocyst (*Ot.*) is buried: lower down, where it makes the clearly defined hinder margin of the sinus, it is composed of cell masses derived from myotomic structures, and is apparently in series with the myotomic ventral downgrowths to be found in the body wall. The first cervical myotome is indicated (*C.* 1) in the figure, and, in line above this, are indefinite suggestions of continuation of the series upwards. Examination of sections shows that these last are indeed myotomic in structure, and have a clearer division into blocks than is apparent on the surface. Cells derived from each of these blocks are found extending into the prominent caudal border of the sinus, making a thick mass lying in a caudo-ventral disposition: the resulting collection of cells shows some slight indication of segmental arrangement (better marked at a later stage) but no sign of this is to be found on the surface. They extend to the pericardium and limb bud, which is not seen in the figure.

The epipericardial ridge, the lower boundary of the sinus field, is composed of cells continuous with and presumably derived from the anterior and deeper parts of these myotomic outgrowths: hence the continuity of this ridge with the caudal boundary of the field. The tract of cells forming the ridge passes forwards and inwards, below and internal to the lower end of the third arch, then internal to the inner and lower end of the second arch: here the tracts of each side lie together, and thence pass into the substance of the mandibular arch, where they become continuous in later stages with the rudiments of the tongue muscles. The hypoglossal nerve is not traceable beyond its origin in the embryo represented in fig. 1, but is found a little later in the ridge with the cell tract. The ridge connects the arches with the pericardium as far forward as the level of the second arch; it rests below on the pericardium, and is only separated by a shallow groove from the arches lying above it.

The relations between pericardium, epipericardial ridge, and outer pharyngeal arches can be understood from fig. 2, which gives a view from below of the region after removal of the pericardial projection: the arches and in fact the whole region are represented as flattened to some extent. The pericardial roof, where it is joined to the neighbouring tissues, is retained. The epipericardial ridge on each side is indicated by interrupted lines lying between the arches and the pericardium. It is seen that, with the exception of the first,

the external arches do not meet their fellows in the middle line, being separated by ridges and pericardium: it may be said at once that they never do meet their fellows in the middle line, the ridge areas and (at first) the pericardium intervening. As the pericardium acquires a more caudal position relative to the arches, the enlarged ridge-tracts come together in front of it, and a central area still separates the remnants of the regions of the arches on each side from each other.

It is to be observed that the ridge-tracts pass internal to the ventral or inner ends of the second and third arches, but in front of this sink into the

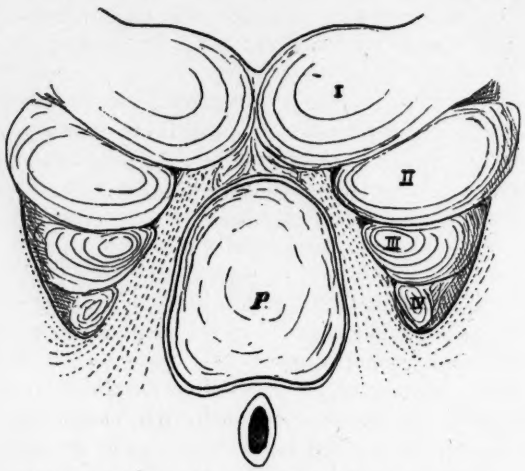


Fig. 2. Semi-schematic view of the lower aspect of the pharyngeal region, the pericardium having been removed, save for its roof. *I, II, III, IV*, pharyngeal arches, external; *P*, roof of pericardium. The whole region is somewhat flattened out to show the relations.

substance of the mandibular arch, which is the only one completely joined in the middle line.

Before leaving the early stage shown in fig. 1 it is necessary to note that there is a fairly broad strip of thickened ectoderm, the placodal area, running from before backwards along the upper ends of the arches and grooves. Without advancing any opinion about the value of this area, it can be pointed out that in certain parts its cells are certainly continuous with the cellular masses of nerve rudiments. Two of these parts, in connection respectively with the rudiments of the IXth and Xth nerves, are of importance from the present point of view: they are indicated by dotted lines in fig. 1, while the rest of the strip, not associated directly with nerve rudiments, is not shown. The IXth placode is at and above the upper end of the third arch, some little distance down the side of the long second groove; the Xth placodal area, perhaps more extensive than represented in the figure, covers the upper and

greater part of the fourth arch, a small area above it, and the whole depth of the paraxial border in this part.

The area of the precervical sinus deepens as the result of rapid growth of its paraxial boundaries, the second arch also becoming more prominent for a time. Fig. 3 (Pl. I), from an embryo of 8 mm., gives an illustration of the earlier consequences of this growth. The main feature is a rapid increase in paraxial mesodermal thickness, which thus comes to overlap and fold in the placodal areas. As a result placodal area IX is now lying at the bottom of a short recess opening into the upper part of the apparent second groove, while the turning in of the large Xth area has led to practically the whole fourth arch being hidden in a similar but larger recess. Between the two recesses the paraxial thickening bulges above, but does not cover or invade, the area of the third arch.

At the point *ep.* in fig. 3, where the growing paraxial region is apposed to the long second arch, there is a very small fusion between these parts on the other side in this embryo; it could not be recognised with certainty on the left side. It suggests a fusion, no doubt associated with the growth which causes the overlapping of the placode here, between the paraxial swelling and the upper part of the hinder border of the second arch.

The upper portion of the second groove, above the level of the placode, is now only represented by a shallow depression. This part has been practically obliterated, but not, it would appear, by any process of fusion: the condition found in an embryo of 7 mm. supports this opinion. In this specimen the paraxial growth is overhanging the placode but has not yet begun to turn it in, and the posterior border of the second arch, clearly cut opposite the placode, becomes shallow and indefinite above this in the region of paraxial thickening. It seems that the level of the depression behind the upper part of the second arch, as far down as the placodal inturning, is simply raised and the edge of the arch made indefinite by the growth of the mass behind it, without any meeting and fusion of the two prominences. If this view of the matter is correct, the very small fusion noticed on one side in the 8 mm. embryo may be nothing but a deceptive appearance, or may be an indication of a definite little point of suture between the arch and the overhanging lip of the growth covering in the placodal area. The fusion, however, if it does occur at all, does not go any further: the conditions shown in fig. 3, in fact, may be said to indicate already what will be the extent of overlapping in the region of the sinus brought about by the surrounding growth.

The sinus field in an embryo of 10 mm. is shown in fig. 4 (Pl. I). The placodal areas are now so completely covered and folded in that each is at the enlarged end of a deep pocket or tunnel opening on the surface. The conditions are essentially as in fig. 3 so far as the positions of the openings of the tunnels are concerned, the only difference being in their sizes: they are both smaller, and lead into deeper recesses, that of *X* being so deep that the fourth arch is no longer actually visible in its floor as in the earlier specimen. The third arch

stands out clearly, and is not overlapped or covered in any way by the formation of these placodal pockets.

It is obvious that the changes going on are concerned mainly with the closing in of the placodal areas. The process is fairly rapid, and by the time that the embryo reaches a length of 12 mm. the areas are shut off from the surface. Intervening stages simply show the intermediate conditions.

Fig. 5 gives the surface view of the region in an embryo barely 12 mm. in length. In this specimen the two placodal areas form buried cysts (*cervical vesicles*) related to the corresponding ganglia. Cyst X is connected with the surface still by a definite epithelial strand, enclosing a lumen at its inner end, but otherwise apparently a solid thin cord: placodal cyst IX has lost its connection with the surface, but the line formerly taken by this can, I think, be made out. The duct of this cyst disappears apparently about the 11 mm.

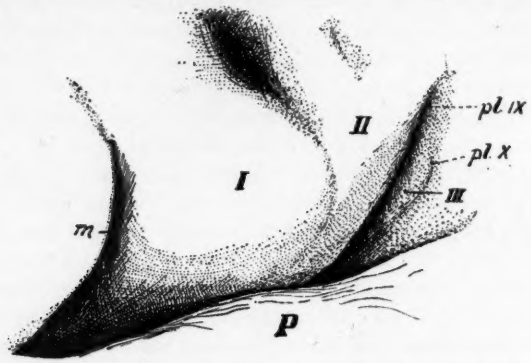


Fig. 5. Left side of region in an embryo of 12 mm. showing the structures behind the mouth, *m.* *I, II, III,* pharyngeal arches; *P,* pericardium. Ectodermal connections with placodal cysts indicated at *pl. IX, pl. X.*

stage. The position of these two points of final attachment to the ectoderm in the 12 mm. embryo can be seen in the figure: the third arch lies, as before, between them, bounded behind by a very shallow but definite groove, and the condition is as in the 10 mm. embryo with the exception that the two open ducts have been closed.

This terminates the history of the surface changes in this region, so far as the sinus is concerned. No further overlapping takes place, nor is it to be expected. The only things that have been covered in in the field of the original sinus are those parts that were related to placodes, and the greater portion of the field—that is, the third arch—remains exposed. The vesicles disappear almost immediately after their connections with the surface have gone.

In this account of the changes taking place in the region of the sinus in the human embryo, the placodal areas certainly stand forward most prominently as the structures that are mainly affected: they are covered in and

sink deeply, and they are the only areas really in which any marked change is brought about, in this or in any other way. It is allowable, of course, to refer their sinking to their connection with nerves which remain in relation with the visceral wall, but one cannot help feeling that there is more in the matter than a mere physical attachment, and that some explanation is required for their persistent existence as open vesicles with "ducts," and for their disappearance when these channels close, as well as for the general fact that they seem to be the centre of the changes which go on in the region under consideration. I can offer no suggestions on the matter: no definite contributions to the nerves were made out, although there was certainly the appearance of contribution to the sheaths of the nerves, but the sections had not been prepared in any special way to show such processes if they existed. One recalls the formation of the organ of Pinkus, or Müller, permanent or temporary placodal derivatives of unknown function: it is possible that the placodal cysts of the present description may represent remnants of parallel formations more caudally situated, but in any case the same unsatisfactory ignorance of possible function must remain.

The disappearance of the third arch as a projection on the surface is easily understood. This arch is concerned in the formation of many important structures in and about the pharynx, but not on the surface, and its appearance on the surface is only the result of its growth and condensation when the wall of the pharynx is relatively thin. As the wall thickens the active growth of the arch, being concentrated in its deep portion, quickly loses its influence on the surface form, and by the time the embryo reaches 12 mm. in length, or even before this, any direct continuity between the surface arch and the deep arch structures cannot be made out in sections: shortly after this the absence of any sort of resistant connection between the two is emphasised by the change in position of the arterial stems in this region, but this change has really begun much earlier and indicates a correspondingly earlier divorce between the internal arch and its external manifestation.

Under these circumstances of failure of the continued action of the growth originally producing it, it is to be expected that the external arch would tend to disappear, and it does this largely by the simple process of flattening. The prominence of an arch depends, however, not only on its own size, but equally on the depths of the grooves that limit it, and this is seen very well in the case of the third arch.

The second groove persists because it is the transverse line of flexure of the neck, whereas the third groove, not very deep in the early stages, begins to get shallow very soon, so that at the 10 mm. stage, for example, the arch is an upstanding structure seen from the front (fig. 6) owing to the depth of the second groove, whereas it is separated from the structures behind it by a very shallow remnant of the original third external groove. In the 12 mm. stage this inequality in accentuation of the margins of the arch is even more striking, and it is evident that the hinder groove is on the point

of disappearing, leaving the surface of the arch continuous with that of the adjoining area.

The grooves were carefully examined with a view to ascertaining the mode of disappearance, so far as this could be done: in this connection I would like to express my thanks to Dr Gladstone for the loan of a couple of embryos, which I examined in addition to my own. The groove between the first and second arches is closed by epithelial fusion at about 11 mm., but in no other part was such method of occlusion to be made out in any way. No epithelial remnants were found at any stage, or in any position, in relation with the other grooves, except of course in the cases of the "placodal ducts."

Fig. 6. Tracing of outlines in pharyngeal region of 10 mm. embryo. *I, II, III*, pharyngeal arches; *ent. iii*, *ent. iv*, 3rd and 4th entodermal pouches.

No definite statements can be made about the *modus operandi* of closure of these channels leading from the placodal cysts, except that they gradually increase in length and decrease in calibre, and in doing so show no sign whatever of any epithelial destruction. Perhaps this really expresses the matter, for it seems possible that increasing thickness and depth of the growing tissues round them would lead to these two changes taking place simultaneously: at any rate the sections failed to afford me any more complete explanation of the changes, and the matter must be left here. The final separation from the surface may be brought about by destruction of the elongated epithelial strand, for what might well be remnants of such a strand could be found in association with placodal cyst IX at 12 mm., although I have not so far been able to recognise at a later stage any remains that might have been associated with the other vesicle.

The flattened external third arch, left exposed in the way described, forms a part of the surface of the neck, but the area made by it can only be arrived at by inference. In an embryo of 13·5 mm. it is possible to find what seem to be the limits of the arch, but after this, although the definite line of transverse flexure is undoubtedly the second groove, there is no way of distinguishing with any certainty at all the caudal boundary of the third arch. At this stage the rudimentary condensation of the clavicle can be recognised, lying in the third arch area just caudal to the transverse flexure line. The constituent tissues of the original epipericardial ridge lie ventral and internal to the third arch area, and can be traced forward to the hyoid rudiment: it is interesting to observe that there is definite continuity between these early muscle fibres and those in the tongue, passing on the ventral side of the hyoid, although most of these fibres below the third arch area end at the hyoid rudiment. Traced backwards, these fibres pass behind the arch area, lying

deep to the sternomastoid, which is now definitely distinct from the deeper structures of the caudal border of the sinus field. There is here, evidently, little more than the differentiation of the tissues in and surrounding the caudal border of the sinus field: there is no alteration in their arrangement, but the appearance of the clavicular and hyoid rudiments afford new standards by which one may appreciate further changes.

The clavicular condensation reaches the middle line just caudal to the flexure line, where it is continuous with the episternal thickening ventral to the upper part of the pericardium: it extends upwards and outwards from this. It is obvious, then, that this condensed region near the middle line

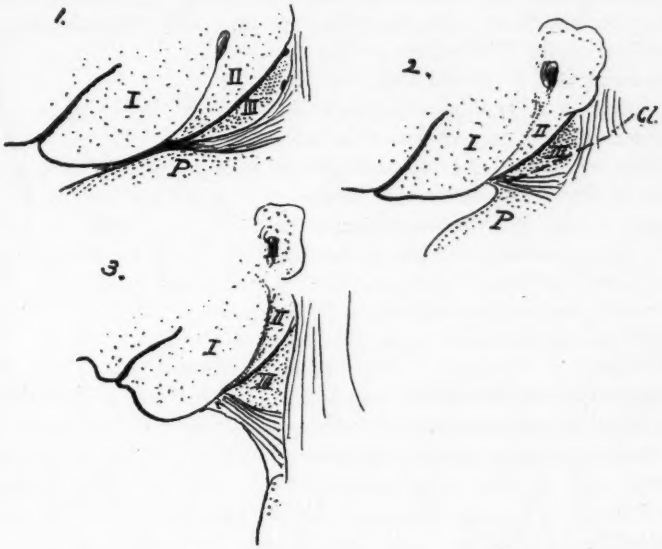


Fig. 7. Three schemes to show the situation acquired by the third arch as the neck forms. *Cl.* gives the general position and line of the clavicle. Other references as before.

is in close relation with the epipericardial structures, which can now be referred to as the infrahyoid muscles, and by the time the embryo reaches a length of 16 mm. the muscle sheet is attached to the skeletal elements. The sections give the impression that the enlarging end of the clavicle has grown into the muscle layer, but whether this is so or not, the attachment of the muscle sheet here is quite evident. The clavicle is practically in the same position as before, and the neck, from the adult point of view, is as yet hardly in existence.

We have here, however, the foundation of the neck, with certain fixed points, and its formation in the second and third months runs the course that might be expected from the facts already stated. It is not necessary to add

to the length of this paper by going into the details of the growth, and it will be enough for present purposes to indicate their general results in the accompanying schemes (fig. 7). The first figure shows the general arrangement of the embryonic parts as detailed earlier in this paper, the epipericardial ridge being lined and the arches numbered. The second scheme shows the same conditions when the clavicular rudiment (*Cl.*) is first present and the sternomastoid is distinct. The result of the lengthening of the neck is given in the third figure. The infrahyoid muscles, fixed to the clavicle and hyoid, are drawn out on the ventral side, the sternomastoid is a fixed structure behind, and the line of flexure marks off the second and first arches in front, so that the third arch area practically corresponds with the skin covering the carotid triangle. I feel no doubt that this is quite correct in a general way, but one cannot affirm that the boundaries of the arch area and the triangle would necessarily correspond in every way. In this connection it is interesting to recall Head's "superior laryngeal" area of hyperaesthesia: it is shown in fig. 8, modified from Head's original diagram, and represents a cutaneous area which might very well correspond with the skin surface of the third arch, extended under the conditions just described. It would not be justifiable, of course, to do more than suggest here such a possibility, but it may be said that Head originally proposed (*Brain*, vol. XVII, 1894) on theoretical grounds an association of the area with the third postoral arch.

Fig. 8. To show the superior laryngeal area (stippled) of Head. Modified from Head's original diagram.

It can be seen that there is no support in embryonic human development for the idea that the sinus is covered in by some modification of an operculum derived, as in those lower forms which possess it, from the hyoid arch. It is evident that this arch enlarges considerably and, as a result, hangs over and thus partly hides the sunken area of the sinus, but this is only a superficial appearance and one of short duration. The second groove, deep and clear, persists throughout as the transverse line of flexure, so that the area behind it remains open, and the enlargement of the second arch is apparently only connected with the primary architecture of the outer ear. The only sign of fusion of the second arch with structures behind it is the doubtful (and in any case very small) closure at its upper part in the 8 mm. stage, not affecting the true sinus area in any way, and no indication of any formation resembling an opercular growth—unless it is the pinna—is apparent. The placodal areas which lie at the bottom of the cervical vesicles seem to be closed in by the

activity of the paraxial mesoderm, and that belonging to the pharyngeal arches appears to be, in this connection, quite passive.

Finally, a few words may be said about the muscle cells in the epipericardial ridge. The upper cells in this ridge, those continuous with the deeper parts of the downgrowths from the occipital myotomes, apparently disappear during the evolutions described in this paper. They seem to do so from behind forward, and this is associated with the appearance of the lingual musculature. This is suggestive, but is not enough in itself to allow one to say that there is an actual migration of cells from the occipital region to the tongue. Nevertheless, the direct association of the intrinsic tongue musculature with the occipital myotomes is evident, even if we cannot certainly affirm that migration takes place from this region during ontogeny.

Vestigial remnants in the neck.

The conditions not uncommonly met with on the side of the neck and frequently termed "branchial rests" are evidently abnormal, and hence postulate some abnormality in developmental processes as underlying their presence. Since the account in this paper of the processes which go on in the sinus area would destroy the conception of a closed sinus, which is accepted as a centre round which the formations radiate, so to speak, it may be permissible to indicate what would seem to be possible sources of the fistulae or cysts that come under this heading. The abnormal processes may be divided into (1) abnormal persistence of normal states, or delayed development, and (2) abnormal processes of development.

(1) The normal formation of ectodermal cavities in association with the sinus region as dealt with in this paper include only the placodal cysts and their ducts: any one or more of these might conceivably persist, either alone or in combination. To these must be added the possibility of persistence of one or more of the ectodermal "external pharyngeal ducts" which are connected with the entodermal pouches: these have not been mentioned in this paper because they are not concerned with the changes in surface appearance of the sinus area, but they are, as is well known, deep prolongations of grooves, and they normally disappear before the final stages of the surface changes are entered upon. Outside the sinus field the first groove closes by epithelial fusion, which might remain as a septum.

(2) Abnormal fusion between the sides of the second groove in some part of its extent would be among the least of possibilities coming under this heading, and one can imagine similar or parallel formations elsewhere: the list could then be extended to conditions of gross abnormality or monstrosity. As in the rest of the body, we are practically quite ignorant of the forces acting behind the surface manifestations, so that it is impossible to imagine along what lines the structures would develop if some small interference with their play were experienced at a very early stage in the evolution of a part: hence one cannot do more than enter these possibilities on the list

in the most general terms. It is possible that those cases in which sinuses are found low down in the neck, for instance between the heads of the sterno-mastoid, may come in this class, although it is not impossible that they may come in (1).

It can be seen, then, that, without calling on a precervical sinus, a very fair list of possible sources of trouble can be made out—but which of the number may really be factors in clinical cases, and which may be nothing more than theoretical figments, I cannot for a moment presume to say.

We come now to a matter more important from an anatomical standpoint, one that bears directly on the position of some of these remnants and affects profoundly the theoretical conception of their disposition, and yet is not taken into account as a rule when these quasi-pathological structures are considered by the clinical pathologist. I refer to the hypoglossal nerve and its course. The nerve lies at first behind the region of arches and grooves, and turns forward along the top of the pericardium: in other words, it lies in the caudal border of the sinus and in the epipericardial ridge. In attaining its ultimate position its loop is drawn up to a higher level and must (being a deep nerve of the body wall) in its transit pass deep to structures connected with the ectoderm, and superficial to all those structures connected with the pharynx. Thus we find it at different stages lying external to pharyngeal pouches and their derivatives, to the carotid vascular system, the hyoid, and the nerves associated with the visceral tube. It is obvious, then, that if any such thing as a connection between the surface and the pharyngeal wall or its derivatives were to persist, the connecting strand would be caught up over the hypoglossal nerve: the same applies, of course, to any connection between the surface and a placodal cyst, which would presumably be in association with its nerve ganglion. Thus every vestigial remnant in the neck that has a deep connection as well as an outer opening would have to pass upward to cross the hypoglossal before it could run to its original deep attachment, and, if such remnants occurred, the existence of deep connecting stalks would seem to be considerably endangered by the transit of the nerve loop. A little consideration of these facts, and remembrance of the changes in position of the nerve, would no doubt lead to more cautious appraisement of the developmental value of vestigial structures when they are encountered.

SUMMARY

1. The appearance and nature of the precervical sinus and its boundaries are described and figured.

2. It is shown that the sinus does not close in the sense usually understood. The fourth arch is covered, but the third arch remains on the surface of the neck, its area possibly corresponding with Head's superior laryngeal area.

3. Placodal areas associated with IXth and Xth ganglia are covered in and form cervical vesicles, opening at first on the surface but not into a

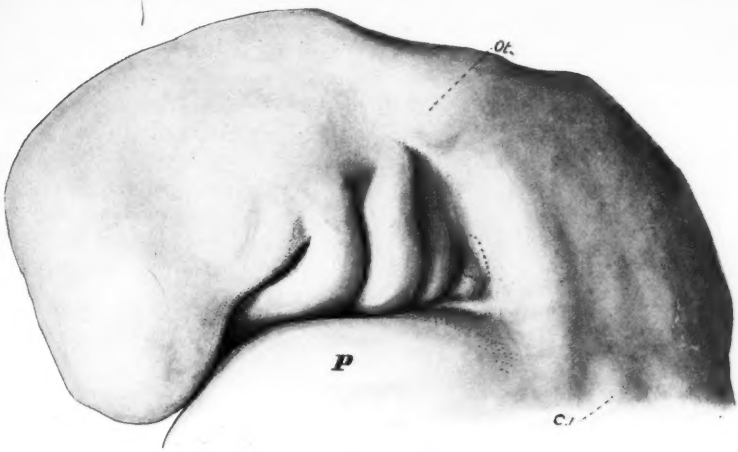


Fig. 1.

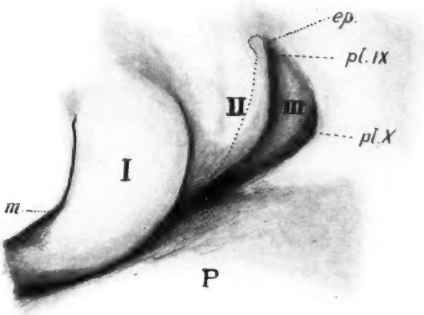


Fig. 3.

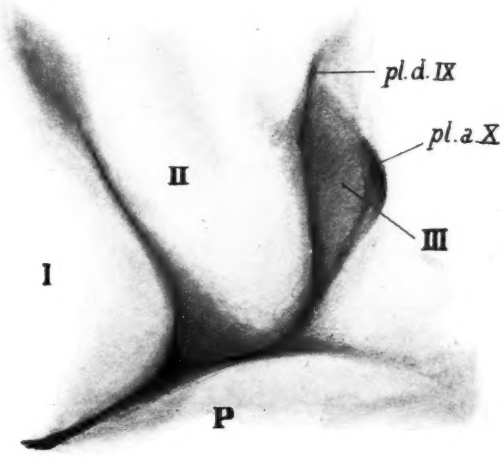


Fig. 4.

UNIV. OF MICH.

common sinus: they close and disappear very soon, and it is in the covering in of the Xth placode that the fourth arch is involved.

4. Infrahyoid and tongue muscles and occipital myotomes are shortly dealt with in so far as they have to do with the formation of the area of the sinus and of the neck.

5. Some possible sources of formation of so-called "branchial remnants" in the neck are suggested, but no attempt is made to give any proportionate value to the suggestions.

6. Attention is called to the necessity of recognising the position, and changes of position in transit, of the hypoglossal nerve when dealing with any such remnants in the neck.

DESCRIPTION OF PLATE I

Fig. 1. Head of embryo of 4·9 mm., seen from the left. *P*, pericardium; *C.* 1, first cervical myotome; *Ot.*, otocyst.

Fig. 3. The precervical sinus in an embryo of 8 mm. seen from the left side. For description see text.

Fig. 4. Region of precervical sinus in 10 mm. embryo. Left side. *P*, pericardium; *I*, *II*, *III*, pharyngeal arches. The widely open placodal recess of vagus, *pl.a.X*, is below and behind the narrow duct, *pl.d.IX*, leading to the glossopharyngeal ganglion. The epipericardial ridge is very prominent below and behind the third arch

IS THE MINGAZZINI PHENOMENON, IN THE VILLUS OF THE SMALL INTESTINE, AN EVIDENCE OF ABSORPTION?

By CHARLES C. MACKLIN and MADGE THURLOW MACKLIN

From the Department of Anatomy of the Medical School of the University of Western Ontario, London, Ontario, Canada

In the year 1900 Pio Mingazzini (1) of Rome described a change in the epithelial cells of the villi of the small intestine of the hen, and interpreted it as evidence of the absorption of foodstuffs. This change consisted in the formation, in the basal portion of these cells, during the time that absorption was proceeding, of small vacuoles (figs. 2 and 3), which quickly became more and more numerous and so caused the region of the cell in which they were situated to elongate, and in time to lose its outlines. Paraphrasing the words of Mingazzini[1], at the base of the cell there was an accumulation of transparent spherules, surrounded by a large-meshed reticulum, which through pressure assumed polygonal outlines. At the height of digestion the subnuclear regions of the cells, when considered collectively, might be likened in structure to a mass of foam, which usually enveloped the tip of the core of the villus like a cap, becoming thinner as it extended down the sides. Upon this fluid accumulation the peripheral nucleated portions of the cells rested. This material, he thought, gradually diminished in volume, and was presumably taken up by the blood vessels and lymphatics, the epithelial cells meanwhile undergoing a shortening which was associated with a return of their outlines in the basal region. The cells thus resumed the condition of rest, in which there was no vacuole collection intervening between the nuclear region of the cell and the base.

This interesting phenomenon, which we shall hereafter refer to as the "Mingazzini phenomenon," suggested to Mingazzini a secreting gland, for the increase and diminution of these vacuoles recalled the production and discharge of granules of zymogen; but here the cells were operating in the opposite direction to that of externally secreting glands, so that he supposed himself to be dealing with a reversed gland, or what was essentially a gland of internal secretion. The villus epithelial cells, he reasoned, must be absorbing materials from the lumen of the gut and transforming them into an "internal secretion" which then passed through the bases of the cells into the environ-

[1] We wish to express to Professor Lewis H. Weed, of Johns Hopkins Medical School, our warmest thanks for the loan of an excellent translation into English by Huiskamp of the Mingazzini article.

ment of the capillaries and lacteals, there to be absorbed. If this "internal secretion" was produced more rapidly than it could be resorbed by the collecting system, then it piled up, so to speak, within the protoplasm of the basal portion of the cell, which lent itself conveniently to this temporary storage by expanding in the manner described: but as absorption from the gut-lumen waned the resorptive mechanism began to overtake its task, and gradually carried away the "internal secretion," which might really be called chyle. The subnuclear foam-structure was, in other words, but a surplus of chyle awaiting removal from the cells, which suffered, apparently, no injury from this periodic swelling and shrinkage for, with the evacuation of the aggregation of vacuoles, at the culmination of a period of absorption, they were ready, apparently, to begin all over again, the cycle being repeated, presumably, with each period of absorption. It seemed that Mingazzini did not limit this phenomenon to an association with any particular food element, though later workers, ruling out fat and carbohydrate, limited it to protein.

Mingazzini was really dealing with something which had been known for many years, and which had been interpreted in different ways. Grünhagen (2) (1887) thought that this sub-epithelial space contained chyme admitted through a hypothetical pore in the epithelium, while R. Heidenhain (3) (1888) and others looked upon it as an artifact due to fixation.

Mingazzini's publications set numerous workers into activity, and the years immediately following were marked by a number of contributions in favour of, and opposed to, his hypothesis: but space will not permit of their being reviewed here. Suffice it to say that considerable doubt has arisen as to the validity of his view, and writers like Luciani (4), who at first accepted the Mingazzini hypothesis, have come to regard his case as not proven. But there seems even at the present time to be a tendency to consider the Mingazzini phenomenon seriously, and we find, for instance, in the 1926 edition of Starling's *Physiology*, on p. 643, the figures of Reuter (5) (figs. 7, 8 and 9) purporting to represent the change in the villus epithelial cell during protein absorption, together with a short account of his views, which are merely modifications of those of Mingazzini, although Starling expresses himself as being doubtful of Reuter's interpretation.

We should say at the outset that the Mingazzini phenomenon may be produced (or possibly we should say simulated) by the use of improper fixatives (fig. 6), such as Flemming's chromic-osmic-acetic mixture, or hot solutions. We partially agree, too, with those workers like Demjanenko (6), who found that it could be avoided by the use of the proper fixative. But our main contribution is that the Mingazzini phenomenon comes on in intestines which are merely allowed to lie for a short time, after the circulation has stopped, before they are fixed. The following is a brief synopsis of some of our experiments.

We studied the intestines of dogs, cats and guinea-pigs, while absorbing either foodstuffs of various kinds, or water alone, and also during starvation,

and in all cases the Mingazzini phenomenon appeared as a post-mortem (or perhaps more accurately, an agonal) change in the villus. The course which we usually followed was to anaesthetise an animal during the height of digestion, and, while the circulation was still vigorous, to remove and fix at once a piece of small intestine, which served as the control. The animal was then killed by bleeding, or opening the thorax, or both; and, at successive intervals after the circulation had ceased, pieces of intestine from regions adjacent to the first specimen were removed and fixed. In this way we had a series of pieces of intestine in which the only variable factor was the length of time elapsing between circulatory arrest and fixation. Such a series often contained some ten or more stages, from the control to that of one hour or more after death. The fixation was the same in each case, of course, and usually consisted in the piece of intestine being slit open and plunged into a cold mixture of 10 per cent. formalin (neutralised with magnesium carbonate) in Ringer's solution. This gave very good results. 10 per cent. aqueous formalin was also satisfactory. In some cases the fixative was injected, while the animal was still alive, into a loop of gut which had been clamped off: then, after a short interval following the death of the animal or clamping off of the mesenteric vessels, the fixative would be admitted to the next section of gut by removal of the first clamp, and this process was repeated until we had a series differing, as before, only in the extent of the delay preceding fixation. The immersion and injection methods gave similar results with respect to the study of the Mingazzini phenomenon. Subsequent technique was, of course, uniform throughout the series. Sections were cut from paraffin at 5 μ and stained in different ways.

In all of the controls the epithelium rested upon the basement membrane, and there was no subnuclear accumulation of spherules such as Mingazzini described, although many of the animals were unquestionably absorbing. This was true of all animals irrespective of the foodstuffs used, which consisted either of the usual diet of the animals, such as milk, bread and milk, and fresh meat, or the elementary foodstuffs—fats, carbohydrates and proteins—which were given after preliminary starvation. It was also true of animals absorbing water alone, as well as of those studied during starvation.

In the intestines of all animals studied by this method the Mingazzini phenomenon appeared after the lapse of a latent period of variable duration —usually between five and ten minutes. The first step was, as Mingazzini had recorded, the appearance of vacuoles in the subnuclear portion of the cell, usually at the tip of the villus: these soon coalesced, and the very thin base of the cell, adhering to the basement membrane, was separated from the main portion, which contained the nucleus. Continued ingress of fluid caused the epithelium to become separated from the basement membrane by a space which often grew quite large, so that we had what has been described as a "ballooning" of the epithelium above the core. These caps of epithelium, in the later stages, might be compared to the empty fingers of a glove (fig. 10). This was merely an extreme case of what Mingazzini had described. We

found that the appearance of the material beneath the epithelial balloon varied with the fixative used, thus with formalin the space was, for the most part, without structure, but contained a small amount of coagulated, vacuolated, eosinophilic material, in which lymphocytes were embedded, while with Zenker-acetic or osmic acid vapour it was foam-like. The progress of the phenomenon was very rapid when it had once started, and it was very difficult to get the initial stages in the sections.

We at first thought that the fluid originated from without—that it was due to continued absorption from the gut after the channels of outlet had been stopped—and it is possible that this may take place, to a slight extent. It became apparent, however, that this theory would hardly account for the latent period which always occurred, and which varied in duration, nor would it explain the very rapid progress of the phenomenon once it got under way. It was apparent that we were dealing, like Heidenhain, with an expression of fluid from the core out through the basement membrane into the surrounding epithelial cell protoplasm, which fractured, apparently, along its line of least resistance. The appearance, at first glance, was as though the epithelium were lifted from the basement membrane, but in all cases there was a very thin film of epithelial protoplasm left attached to the basement membrane, proof that the cell had actually ruptured. The contraction of the villus core was doubtless the work of the smooth muscle within it, which might be presumed to be stimulated by the condition of asphyxia supervening.

The phenomenon occurred not only in conditions of absorption, but also of complete rest. There seemed to be no difference related to the kind of food which was being absorbed, except in the duration of the latent period, and the rapidity of progress and extent of the process. Thus, with solutions of pure dextrose, it was delayed in onset, and was slight in degree. When 10 per cent. dextrose was given through a stomach-tube to a previously starved cat, no Mingazzini phenomenon had occurred in the jejunum at the end of an hour, but in the duodenum of the same animal it was well marked at that time. We attributed the long latent period here to the high osmotic pressure of the material in the lumen, and to the dehydrated condition of the villus core associated therewith.

Such a series of intestinal material presented a graphic picture of the progress of the Mingazzini phenomenon, and proved conclusively, we think, that it is, in its earlier stages, nothing but an agonal change, and, later on, a post-mortem change. After an epithelial balloon has formed it falls over, becomes partially collapsed and soon disintegrates, and the end result is the well known picture of isolated epithelial cells and often irregular and more or less complete rings of epithelium, minus the core, as seen in sections. Such pictures have proved a puzzle to histologists, and also to pathologists, who have become familiar with them in human material from autopsies.

We have noted that an improper fixative may produce a sub-epithelial space like that of the Mingazzini phenomenon, when used upon material

taken even while the circulation was intact. On material taken after the onset of the Mingazzini phenomenon, such fixatives would give a picture in which the shrinking action of the fixative would be superimposed upon the agonal change.

We should add that we made a thorough inspection of living villi of animals, in which the blood was circulating, and which were at the height of digestion, and in none of them could we find, by the aid of a powerful binocular microscope and suitable illumination, any indication of the Mingazzini phenomenon. We also made a number of observations in isolated loops of intestine containing various solutions, from which it was plain that the Mingazzini phenomenon was conditioned by circulatory arrest.

We can, then, answer our question in the negative: the Mingazzini phenomenon is not an evidence of intestinal absorption. It is an agonal or post-mortem change, and does not occur, under normal conditions of life, in the intestinal villus. No one, apparently, had realised that such a profound cytological change could take place so rapidly, but when we say that the phenomenon appeared in one of our cases in less than three minutes, and very frequently in from five to ten minutes, it will be realised that, in the course of ordinary laboratory technique, it would have come on before the tissue was fixed, and then, even with ideal fixatives, the villi would show it. There are doubtless a multitude of other instances where artifacts have led to erroneous conceptions and baseless hypotheses. We want the truth about protoplasm —about cell structure—and to gain it we must clear away all technical manipulations which distort the cell substance.

BIBLIOGRAPHY

(1) Mingazzini, Pio (1900). "Cambiamenti morfologici dell' epitelio intestinale durante lo assorbimento delle sostanze alimentari." *Richerche fatte nel Laboratorio di Anatomia normale d. R. Universita di Roma*, vol. viii, pp. 41–64. "La secrezione interna nell' assorbimento intestinale." *Ibid.* pp. 115–30.

(2) Grünhagen, A. (1887). "Ueber Fettresorption und Darmepithel." *Arch. f. Mikr. Anat.* Bd. xxix, S. 139–46.

(3) Heidenhain, R. (1888). "Beiträge zur Histologie und Physiologie der Dünndarmschleimhaut." *Archiv f. d. ges. Physiologie* (*Pflüger*), Bd. xliii, Supplement, pp. 1–103.

(4) Luciani, Luigi (1913). *Human Physiology*, translated by Frances A. Welby into English. Macmillan and Co., Ltd., London. Vol. ii, pp. 294–7. (This gives some of Mingazzini's figures, and a short account of his findings and theory. In our opinion Luciani's version of Mingazzini's histological findings is somewhat inadequate.)

(5) Reuter, Karl (1903). "Ein Beitrag zur Frage der Darmresorption." *Anat. Hefte*, Bd. xxi, No. 1, pp. 123–44.

(6) Demjanenko, K. (1909). "Das Verhalten des Darmepithels bei verschiedenen funktionellen Zuständen." *Zeitsch. f. Biol.* Bd. lii, pp. 153–87.

(7) Tavernari, F. (1916). "Quelques aspects de la villosité intestinale dans la période de l'absorption." *Arch. ital. de Biol.* pp. 313–23. Same article in *Bullettino delle Scienze Mediche*, anno lxxxvii, Serie 9, vol. iv, 1916, pp. 245–53.

DESCRIPTION OF PLATE

This plate shows a group of figures collected from the literature, in which the "Mingazzini phenomenon" is represented.

Figs. 1, 2 and 3 are from the work of P. Mingazzini, and were reproduced in the well-known *Human Physiology* of Luciani (see Welby's English edition, 1913, pp. 295–7).

Fig. 1 represents a villus from the small intestine of the hen in the condition of rest. It will be noted that there is no accumulation of material in the basal portions of the cells, and that the core is not retracted.

We find that this condition is the rule, not only during rest, but also during absorption, provided fixation is immediate, and the fixative one which does not provoke shrinkage.

c. Striated cuticular border of the epithelium.
nc. Nuclei of the cylindrical epithelium.
l. Leucocytes.
mb. Basal membrane.
cv. Adenoid tissue of the villus containing fasciculi of smooth muscle.
vl. Lymphatic vessel.

Fig. 2, according to Mingazzini, represents the condition of a similar villus during absorption. It will be noted that the cells have become much enlarged, particularly in the subnuclear zone, by an accumulation of material, *si*, *zj*, which is described as vacuolar. This is looked upon by Mingazzini as material absorbed from the lumen of the gut and described as an "internal secretion"; he thought that it had become accumulated in this region, awaiting removal by the blood vessels and lymphatics. According to our own observations, such a condition is an artifact, often occurring as an agonal or early post-mortem change, and is not found if immediate fixation with a suitable fixative is done.

Fig. 3, according to Mingazzini, represents a still more advanced stage of absorption in the same type of villus. This, in our view, is only a more advanced stage of the degenerative change which has begun in fig. 2, and would go on to even greater proportions.

Figs. 4 and 5 are from the work of Tavernari, and show a similar artifact to that illustrated by Mingazzini, only much more advanced.

Fig. 4 is from Tavernari's fig. 1, p. 315, and represents, according to this worker, the villus from the first portion of the jejuno-ileum of an adult cat, killed three hours after a liberal meal. In the basal third the appearance is normal, there being a connective tissue axis or core, surrounded by epithelium. In the apical two-thirds, however, there is no trace of connective tissue. It is constituted only of epithelium. Tavernari speaks of this as enclosing a "lymphatic space," and thinks that this phenomenon is part of the absorption process.

Our preparations include a great many conditions just like this, in which the core has retracted and the tube of epithelium which formerly covered it has become collapsed. A few minutes later (if fixation had not been done) it would have been found disintegrated. We would interpret it as a case of delayed fixation.

Fig. 5 (from fig. 2 of Tavernari) shows a small area from the same villus, at the tip of the retracted core (seen within the small square in fig. 4), highly magnified. The "lymphatic space" of Tavernari is seen to be partially filled with a coagulum containing lymphocytes. This is a very common finding in our own preparations. As R. Heidenhain pointed out, this material has probably been squeezed from the core, due to contraction of the smooth muscle. The phenomenon is an artifact, and in no way part of the absorption process. The epithelium of the cap is somewhat thinned, as often occurs in our own preparations.

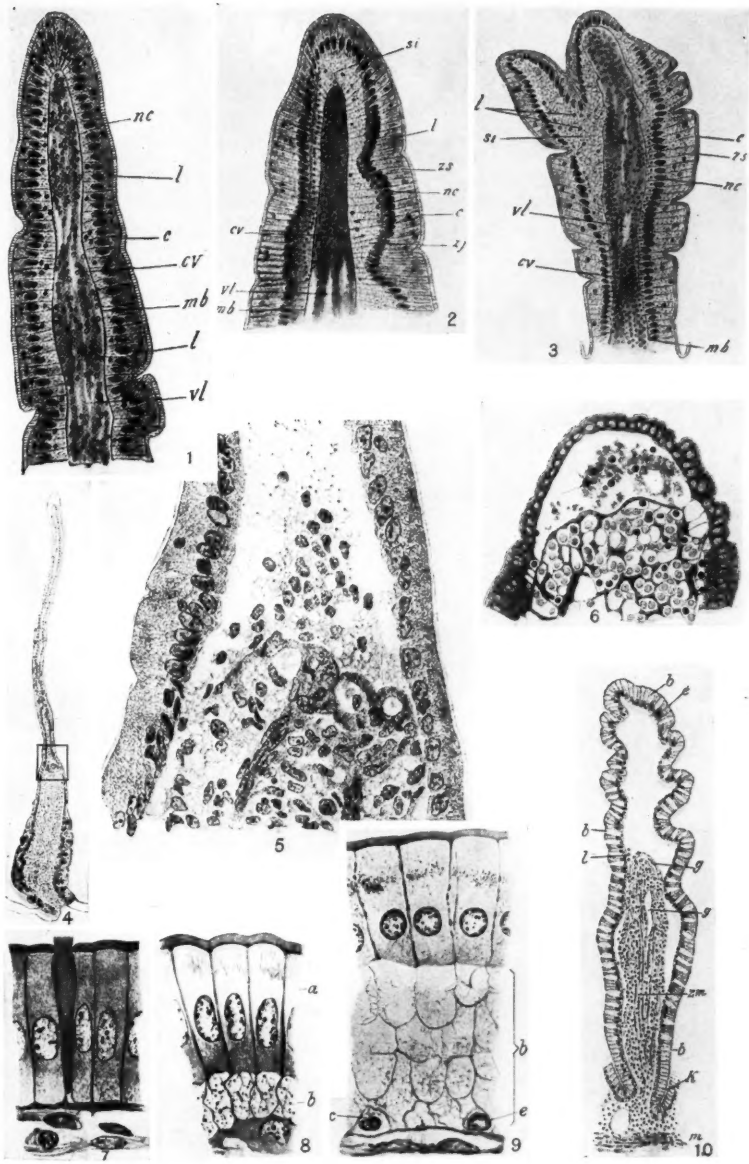
Fig. 6 is from fig. XI of R. Heidenhain. He describes it as epithelium from the surface of the villus of a dog. As a consequence of the immersion of this mucous membrane in a solution of picric acid, the muscle of the villus has contracted strongly, and has caused the coagulable fluid of the core, together with some leucocytes, to be squeezed out under the epithelium, which has been elevated, and the cells stretched. They are quite low and broad, in contrast to the narrower and higher cells which remain clinging to the basement membrane. We have noted similar conditions as the result of the action of fixatives, and thus agree with Heidenhain. We find, however,

that such appearances can occur even with ideal fixation, by merely allowing time to intervene between the stopping of the circulation and the treatment with the fixative.

Figs. 7, 8 and 9 are from the article of Reuter (1903), and were reproduced in Starling's *Physiology*, 1926 ed., p. 643. They purport to show the resting condition of the villus epithelium (fig. 7); early absorption of protein (fig. 8), and an advanced stage of absorption of protein (fig. 9). We would interpret them in a similar manner to the figures of Mingazzini (figs. 1, 2 and 3). Figs. 8 and 9 are artifacts, in our opinion, and we have never found such conditions in normal absorbing villus epithelial cells.

Fig. 10 is taken from fig. 981 of the *Handbuch der Gewebelehre des Menschen* of A. Koelliker, 6th ed., 1899, 3rd vol. by Victor v. Ebner. It is described as representing a longitudinal section through a human villus. The core tissue has become retracted, leaving a large space under the epithelium.

In our opinion it is an advanced stage of the same phenomenon shown in figs. 2, 3, 8 and 9, and is like fig. 4, except that the epithelium is not so much collapsed. It is probably due to delayed fixation. A longer delay would have resulted in the disintegration of the epithelial cap.


nc
l
c
cv
mb
l
vl
1
st
l
zs
nc
c
zj
cv
vl
mb
2
l
st
c
zs
nc
vl
cv
mb
3
4
5
6
a
b
7
8
b
c
e
9
b
g
g
zm
b
K
m
10

UNIV. OF MICH.

REVIEWS

Lehrbuch der Topographischen Anatomie. By JOHN BLUMBERG, University of Dorpat. (Berlin: Urban and Schwarzenberg, 1926.). Pp. 486. Figures 152.

It must always be difficult for the author of a work on Applied Anatomy to preserve the balance between anatomical fact and surgical procedure, but, on the whole, the book under review succeeds in doing so with admirable fairness. In his preface, the author likens the production of a new book on this subject to the putting of old wine into new bottles, but the simile is not altogether apposite, and certainly gives no indication of the thought and time which must have been expended in presenting the subject matter in its present form, and in incorporating the applications of anatomical fact to modern surgery. The book is obviously intended for the student of surgery, both before and after qualification, and it expressly excludes much of the detail which many, if not most, of the teachers of Human Anatomy, the world over, regard as of value in the preliminary stages of a scientific education. It more than fulfils its purpose.

The book deals with the subject regionally, and the Back and Spinal Cord occupy a separate section which is enriched by three admirable diagrams, of great practical value. The common developmental anomalies, and most of the "set" surgical operations, are fully described from the anatomical point of view, and even such a rare procedure as the extirpation of a suprarenal is dealt with in some detail. Possibly more space might have been allocated, with advantage, to the incisions utilised for opening the abdominal cavity, and the way in which they must be governed by the anatomy of the abdominal walls and by the behaviour of the lower intercostal nerves.

The illustrations are numerous, and reach a high standard. They may not, in some instances, possess the same artistic value as those found in some other German and English Text-Books—certainly the illustrations of the brain do not attain to the same level of excellence as the others—but they are clear, instructive, and of practical value. Many of them are distinctly novel and proportionately useful, and certain minor inaccuracies, which are probably unavoidable in a first edition, do not detract in any way from the value of the work, which will prove a distinct addition to the surgical and anatomical literature of any library.

Handbuch der biologischen Arbeitsmethoden: Unter Mitarbeit von über 600 bedeutenden Fachmännern, herausgegeben von Geh. Med.-Rat Prof. Dr EMIL ÄBERHALDEN, Direktor des Physiologischen Institutes der Universität Halle a. d. Saale. (Berlin: Urban and Schwarzenberg, 1926.)

No work which has appeared in recent years foreshadows so forcibly what the growth of science means to publisher and to enquirer as does the one which receives this brief notice. Every department of knowledge must continue to expand; so must its literature; the possibilities of the future are

limitless. Here we are, only in the third decade of the twentieth century, and already Biology requires 200 monographs or volumes and an army of 600 workers to expound merely the methods of enquiry used in modern biological laboratories. Were the facts elicited by these methods to be also collected, systematised and published a library of volumes ten times the size of those contained in the present series would be required. It needs no effort of imagination to realise what publisher and researcher will have to face a century hence, for the rate of increase becomes infinitely more rapid with each additional decade.

It is now as it was before the war—the scientists and publishers of Germany lead the way, for this Biological Text-book is a colossal forecast as well as a most useful present enterprise. Many of the volumes are only remotely connected with the needs of anatomists but two parts or monographs, which have reached us recently, deserve the attention of the readers of this *Journal*. One is entitled the *Methoden zum Studium der Funktionen der einzelnen Organe des tierischen Organismus* (pp. 195, price 11.10 Marks), and represents part 3 of volume III A, of Division V of the combined work. In this part the methods which have been employed to elicit the functions of the adrenal glands are dealt with by Dr Ernst Gellhorn, those for the thyroid by Dr Isaac Abelin, those for the pituitary by Dr Paul Trendelenburg and those for the testis and ovary by Dr Alexander Lipschütz. All of these glands are concerned in shaping structure and in this respect their actions have a direct interest for anatomists. With the exception of Dr Lipschütz these authors are mostly concerned with hormones which have an immediate effect on the functions of the organism and have little to say concerning the rôle they play in regulating growth—particularly in the case of Dr Trendelenburg. Dr Lipschütz, on the other hand, gives growth changes his chief attention.

The other part which we would draw attention to now forms part 2 of Division VII, which is to be devoted to *Methoden der Vergleichenden morphologischen Forschung*, the present part, written by Dr J. Ulrich Duerst, being devoted to *Vergleichende Untersuchungs-Methoden am Skelett bei Säugern* (pp. 200, price 19.80 Marks). Dr Ulrich is a devoted follower of Prof. Karl Pearson and gives precise instructions for measurements of the bones of the skeletons of various mammalian types and makes his methods easily followed by the use of clearly drawn illustrations. For the descriptive record of a dog's skeleton about 1000 measurements have to be taken and an almost equal number of indices calculated. It is when we see science branching out so extravagantly in a field which has no limit that one hopes and believes that an easier, briefer and equally effective way may yet be discovered of studying the form and uses of bones. Still, if one would know what the modern biometrical ideal is, the searcher will find it in this volume.

QUARTERLY JOURNAL OF EXPERIMENTAL PHYSIOLOGY

Editors

E. SHARPEY-SCHAFER (EDINBURGH) W. D. HALLIBURTON (LONDON)
C. S. SHERRINGTON (OXFORD) E. H. STARLING (LONDON)

Vol. XVI No. 3

CONTENTS

M'CREA, E. D., B. A. M'SWINEY, and J. S. B. STOPFORD. The Effect on the Stomach of Section of the Vagi Nerves.—PONDER, ERIC, and ZERED M. FLINN. Studies on the Arneth Count. I. The Relation between Phagocytosis and Nuclear Configuration.—PONDER, ERIC. Studies on the Arneth Count. II. The Relation of Nuclear Configuration to Nuclear Area.—PONDER, ERIC, and K. NEWSTEAD FLINT. Studies on the Arneth Count. III. The Effect of Thyroidectomy.—PONDER, ERIC. Studies on the Arneth Count. IV. The Deflection of the Count by Thyroid Injections.—PONDER, ERIC. Studies on the Arneth Count. V. The Steady State.—SHARPEY-SCHAFER, E., and A. D. MACDONALD. The Action of Extracts of the Posterior Lobe of the Pituitary Body on the Pulmonary Circulation.—KENNEDY, WALTER P. Reproduction and Diet in the Rat.—M'DOWALL, R. J. S. On the Nervous Control of Respiration.

The price of this NUMBER is TEN SHILLINGS and SIXPENCE

Papers for publication may be sent to any of the Editors

CHARLES GRIFFIN & COMPANY, LIMITED

42, Drury Lane, London, W.C. 2

Entered at New York Post Office as Second Class Matter 1925

APHASIA

& KINDRED DISORDERS OF SPEECH

By HENRY HEAD, M.D., LL.D.Edin., F.R.S.

IN TWO VOLUMES. CROWN 4to

£3. 3s. net

(NOT SOLD SEPARATELY)

Volume I contains an historical sketch of the progress of our knowledge in this subject, an account of the new methods of examination employed by Dr Head, and the results of his clinical observations. Further sections are devoted to the question of cerebral localization of function and to novel theoretical conclusions as to the nature and causes of Aphasia, which form a contribution to the problem of the relation of mind and body. Volume II is devoted to a series of clinical reports of cases each of which illustrates one or more aspects of the problems dealt with in Volume I.

Cambridge University Press, Fetter Lane, London, E.C. 4